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STUDIES IN ARTOCARPUS AND ALLIED GENERA,[1] I. GENERAL CONSIDERATIONS

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MEMBERS OF THE GENUS *Artocarpus* are the most commonly encountered representatives of the Moraceae in the lowland forest of the Old World tropics (Africa excepted) apart from the ubiquitous *Ficus*. The genus also includes two important food-plants, the Breadfruit (*A. incisus*) and the Jack (*A. heterophyllus*), which now have a circumtropical distribution as cultivated plants, owing to the efforts of man, which include, of course, the well-known voyage of Captain Bligh ending in the mutiny on the *Bounty*. The fruits of a number of other species are edible, some being planted for the sake of these, and many species provide valuable timber, although they do so in general as scattered members of the forest flora, for the only example of gregarious behaviour is that of *Artocarpus incisus* (probably little, if at all, modified from the original form) acting as a dominant member of the forests of the river-swamps of New Guinea.

The genus *Artocarpus* is singled out by its compound fruit or syncarpium, which attains a large size in some species, notably in the two cauliflorous species, the Jack and the Chempedak (*A. integer*, frequently cultivated in Malaysia). The structure of this fruit has been the subject of special attention in this study with the object of determining the differences between it and the syncarpous fruits of two other small genera of the same area and alliance, *Parartocarpus*, which has frequently been confused with *Artocarpus*, and *Hullettia*, which has proved, somewhat unexpectedly, to show a relationship with *Parartocarpus*, having previously been placed in a different subfamily of Moraceae. A third small genus, *Prainea*, which is more closely related to *Artocarpus* than either of these, although the female inflorescence is not a syncarpium, is also included. It provided another immediate problem, since details of the leaf anatomy had led an earlier author (Renner, 1907 [2]) to unite *Prainea* with *Artocarpus*, necessitating a re-evaluation of his work and its extension to cover all the species here

[1] This series of papers is based on a thesis presented to the University of Cambridge, England, in July 1956 for the degree of Ph.D.

[2] The dates refer to the bibliography at the end of the paper.

recognized, from which it has been concluded that his action was not justified.

The four genera to be included in this study are thus *Artocarpus* J. R. & G. Forster, which is here recognized as consisting of about fifty species, *Prainea* King (four species), *Parartocarpus* Baillon (three species) and *Hullettia* King (two species). They are lactiferous trees or, less commonly, shrubs restricted in general to the lowland tropical evergreen forest of the Asiatic-Malaysian region although some species may extend to slightly higher altitudes or into areas of deciduous forest. A few of the latter are restricted to regions with a distinct dry season and are themselves either deciduous or evergreen, but the rest are merely tolerant of a short dry season, often adopting the deciduous habit when they grow in such a climate.

With an African genus, *Treculia* Decaisne ex Trécul, which has perhaps six species, they form a group within the Old World Moraceae characterized by condensed, capitate, unisexual inflorescences which is sufficiently distinct to justify independent study, although it cannot be entirely certain that it represents a natural assemblage of genera. These genera have been assigned to the subfamily Artocarpoideae tribe Artocarpeae and, as will be shown later, constitute the Old World members of this tribe. Although the three subfamilies of the Moraceae — Moroideae, Artocarpoideae and Conocephaloideae — which are distinguished by the position of the ovule and of the stamens in bud, may be valid groups if some exceptions are allowed for, it is not felt that the present classification of the Moraceae offers a sufficiently satisfactory basis for a detailed discussion of the position within the family of the genera being studied, and there will be given only a brief review of Bentham and Hooker's classification of the Artocarpeae. Full revisions of *Prainea*, *Artocarpus*, *Parartocarpus* and *Hullettia* will be given, in this order, in subsequent papers, while in this introductory paper the more general problems of the generic distinctions will be considered.

The genus *Artocarpus* was described by J. R. & G. Forster in 1776 and has been monographed as a whole once before in 1847 by Trécul, who established two subgenera, *Jaca* and *Pseudojaca*, which are here maintained (the former as subg. *Artocarpus*), on the basis of "alternate" (i.e., spiral) *vs.* distichous arrangement of the leaves and amplexicaul *vs.* non-amplexicaul stipules, as well as on a character of the male flowers which later proved untenable. *Parartocarpus* was described by Baillon in 1875, but was not very clearly distinguished by him from *Artocarpus*, and when King monographed the species of *Artocarpus* in India and the Malay Peninsula in 1889, he included unawares two species of *Parartocarpus*, the discordant characters of which led him to reject Trécul's subgenera. King had also described *Prainea* and *Hullettia* in 1888 but, mistaking the position of the ovule, he assigned them to the Conocephaloideae. In 1902 Beccari published an account entitled "Nuove specie di *Artocarpeae* Malesi e Papuane" in which he pointed out the affinity between *Prainea* and *Artocarpus* and briefly commented on the differences between the latter and

Parartocarpus. The final paper of major importance in the classification of the genera is Renner's study of the leaf anatomy of the Moraceae: Artocarpoideae and Conocephaloideae, published in 1907. Renner re-established Trécul's subgenera but treated them, together with *Prainea*, as three sections under *Artocarpus*, a proceeding which might be justifiable on the basis of leaf anatomy alone, but not if the inflorescence structure is also taken into account.

Various observations had thus been made on the differences between *Artocarpus*, *Prainea* and *Parartocarpus*, but the status and distinguishing characters of the genera had not been fully elucidated, nor had the true affinities of *Hullettia* previously been noted. Although the inflorescence structure of these genera is complex and its morphological derivation is not immediately apparent, no study of the development had been made, apart from a few superficial observations published by Baillon in 1863.

In this introductory paper the results of studies carried out in the course of this revision on the morphology and development of the inflorescences are described and their significance is discussed. Other characters that have been found to be of importance at the generic level, namely, seed structure and germination, shoot morphology and leaf anatomy are then considered. Reference is made as necessary to the work of earlier authors, but fuller historical accounts will be found under each genus. Before entering on the more detailed discussions a summary follows of the characters of these four genera, with their resemblances and differences as established in this survey, and a brief review of their position within the Moraceae.

The genera included in this study have condensed, unisexual, usually many-flowered, axillary inflorescences. (In *Parartocarpus* occasional abnormal inflorescences are bisexual.) The flowers are sessile upon or sunken into a pulvinate, globose, or cylindric, fleshy receptacle bearing interfloral (*Prainea* and *Artocarpus*) or involucral (*Parartocarpus* and *Hullettia*) bracts, the (upper) surface of the receptacle being completely covered. They have no rudiments of the organs of the opposite sex. The stamens or ovaries are enclosed in tubular or 2–4-lobed or -partite perianths (*Prainea* and *Artocarpus*) which may fuse partially or completely to form a syncarpium (*Artocarpus*), or they are sunken in cavities in the receptacle (*Parartocarpus* and *Hullettia*). If the latter, the anthers or styles are exserted either between indurated processes covering the surface and (?) representing perianths (*Parartocarpus*), or through simple perforations in the naked receptacle (*Hullettia*). The male flower has one (*Prainea* and *Artocarpus*), two (*Hullettia*) or up to three (*Parartocarpus*) stamens, which are erect in bud, and the female flower has a unilocular ovary with a pendulous ovule and a simple or bifid style. The seeds and embryos are large with little or no endosperm and no period of dormancy. The embryo has either equal or unequal, appressed cotyledons, and is straight (*Prainea*, *Artocarpus* and *Hullettia*) or curved, the cotyledons being folded just above the base and incumbent (*Parartocarpus*). Germination (otherwise unknown) is hypogeal in *Artocarpus* and epigeal in *Parartocarpus*. The leaves are penninerved (except in *Artocarpus altissimus*) with microscopic epi-

dermal gland-hairs providing characters of taxonomic value and (in *Prainea* and *Artocarpus* subg. *Artocarpus*) resin-containing cells in the mesophyll. They are spirally (*Artocarpus* subg. *Artocarpus*, *Parartocarpus* and *Hullettia*) or alternately and distichously (*Prainea* and *Artocarpus* subg. *Pseudojaca*) arranged with paired or (in *Parartocarpus*) single stipules enclosing the terminal bud (amplexicaul in *Artocarpus* subg. *Artocarpus*, acicular in *Hullettia*).

From this brief account the more important distinguishing characters of the genera may be derived. In *Prainea* and *Artocarpus* the stamens and ovaries are enclosed by perianths, usually mixed with interfloral bracts, and a clearly differentiated involucre is lacking. The embryo is straight, or nearly so, and in *Artocarpus* germination is hypogeal, with no elongation of the hypocotyl. The primary difference between the genera is that in *Prainea* the perianths in the female inflorescence remain free, but in *Artocarpus* they are fused with each other to form a syncarpium, though the fusion usually occurs only in the superficial layer, leaving the perianths free at the level of the ovary. The subgenera of *Artocarpus* can be distinguished from each other and from *Prainea* by the characters of the shoot. In *Artocarpus* subg. *Artocarpus* the leaves are spirally arranged on the shoot with large amplexicaul stipules leaving annulate scars, while in subg. *Pseudojaca* and *Prainea* they are alternate and distichous with small lateral stipules; but the epidermal gland-hairs of *Prainea* and *Artocarpus* subg. *Artocarpus* have multicellular heads and the mesophyll contains resin-cells, while in *Artocarpus* subg. *Pseudojaca* the heads of the gland-hairs are usually unicellular and the mesophyll lacks resin-cells.

In *Parartocarpus* and *Hullettia* the stamens and ovaries are enclosed in cavities of the receptacle, the walls of which have been shown in the former to be intercalary in origin, and there is a well developed involucre of bracts which are basal in *Parartocarpus* and vary to an equatorial position in *Hullettia*. In *Parartocarpus* the embryo is curved, having the appressed cotyledons folded just above the base and incumbent, and germination is epigeal, the hypocotyl elongating markedly and carrying the cotyledons well above the ground, where they separate and become green. In this genus the surface of the inflorescence is armoured from indurated processes some of which are fused basally around the openings to the cavities in the receptacle. This suggests that they represent perianth segments, but their similarity to the interfloral bracts of the allied but less reduced African genus *Treculia* indicates that they may be derived from the latter. In *Hullettia* the fleshy receptacle is naked and both perianths and interfloral bracts appear to be completely absent. The shoot has spirally arranged leaves in both genera, but in *Parartocarpus* each leaf has a single triangular, intrapetiolar, non-amplexicaul stipule (distinguishing the genus from species of *Artocarpus* subg. *Artocarpus* in which the syncarpium is superficially similar), whereas in *Hullettia* the stipules are paired, lateral and acicular.

Within the subfamily Artocarpoideae of the Moraceae, which is characterized by the erect position of the stamens in bud and the pendulous

ovule (compared with incurved stamens in the Moroideae and the erect ovule of the Conocephaloideae), these four genera, together with *Treculia*, represent the Old World members of the tribe Euartocarpeae of Bentham and Hooker (now to be written as Artocarpeae).[3] These authors also included *Cudrania*, which should have been assigned to the Moroideae and will not be considered further, and *Balanostreblus*, which has been shown (Jarrett, 1958) to be based on a species of the South American genus *Sorocea* introduced into the Botanic Garden, Calcutta.

The classification of the Moraceae is still fundamentally that of Bentham and Hooker (1880) and it may be in some need of revision, since the New World genera of the Artocarpeae do not appear to be closely related to those of the Old World. However, the latter form a fairly well-defined group, characterized by capitate, many-flowered inflorescences in which the flowers completely cover the surface of the receptacle (i.e., without the naked strips found in some American genera), and in which there were probably originally both interfloral bracts and a basal involucre. *Treculia*, which is the least reduced genus, is the only one to have both interfloral and involucral bracts well developed, as well as perianths enclosing stamens and ovaries. There is also a rudiment of the ovary in the male flower. It is allied with *Parartocarpus* by the presence of an involucre and the orientation of the embryo. Nevertheless, it must be realized that there is nothing except general similarity to justify the classification of *Prainea* and *Artocarpus* with *Treculia, Parartocarpus* and *Hullettia*; the superficial resemblance of the syncarp in *Artocarpus* and *Parartocarpus* is due to parallel evolution.

The study of this group was suggested to me by Mr. E. J. H. Corner, and was carried out under his guidance at the Botany School, Cambridge, England. I should like to record my grateful appreciation of Mr. Corner's continued and stimulating interest in the research and I am further indebted to him for the use of his notes made in Malaya on field characters and details of seed structure and germination. In addition, numerous specimens of inflorescences preserved in alcohol, which had been collected by him, were loaned for study from the Botanic Gardens, Singapore. These, together with preserved material sent from Kebun Raya, Bogor, Indonesia, and by Mr. T. B. Worthington, Peradeniya, Ceylon, and Mr. G. R. Proctor, Science Museum, the Institute of Jamaica, Kingston, Jamaica, were of great value in studying the structure of the inflorescences. Mr. Chew Wee Lek, now at the Botany School, Cambridge, also generously made available to me inflorescences and young seedlings of *Treculia africana* Decaisne ex Trécul preserved in alcohol which he had collected in Singapore. Seeds of various species of *Artocarpus* were kindly sent for germination by the director of the Botanic Gardens, Singapore.

[3] Actually *subtribe* Euartocarpeae of *tribe* Artocarpeae of Bentham and Hooker, but the ranks and suffixes of these subdivisions have been altered to accord with the modern practice of treating their "Urticaceae" as consisting of the Ulmaceae, Moraceae, Cannabinaceae and Urticaceae (s.s.).

The material which has been examined in the course of this revision is that in the following herbaria:

Arnold Arboretum, Harvard University, Cambridge, Mass. (A)
British Museum (Natural History), London, England. (BM)
Herbarium Bogoriense, Bogor, Java, Indonesia. (BO)
Botanical Museum and Herbarium, Copenhagen, Denmark. (C)
Indian Botanic Garden, Calcutta, India. (CAL)
Botany School, University of Cambridge, England. (CGE)
Forest Research Institute and Colleges, Dehra Dun, India. (DD)
Herbarium Universitatis Florentinae, Firenze, Italy. (FI)
Gray Herbarium, Harvard University, Cambridge, Mass. (GH)
The Herbarium, Royal Botanic Gardens, Kew, England. (K)
Rijksherbarium, Leiden, Netherlands. (L)
New York Botanical Garden, New York. (NY)
Muséum National d'Histoire Naturelle, Laboratoire de Phanérogamie, Paris. (P)
Philippine National Herbarium, Manila, Philippines. (PNH)
Sarawak Museum, Kuching, Sarawak. (SAR)
Herbarium of the Botanic Gardens, Singapore. (SING)
Botanical Museum and Herbarium, Utrecht, Netherlands. (U)
U. S. National Museum (Department of Botany), Smithsonian Institution, Washington, D. C. (US)

Thanks are due to the directors and staffs of these institutions for the loan of material and also for hospitality at the British Museum (Natural History), The Herbarium, Kew, the Rijksherbarium, Leiden, the Muséum d'Histoire Naturelle, Paris, and the Botanical Museum and Herbarium, Utrecht.

The work on which this revision is based was carried out during the tenure of a Maintenance Grant from the Department of Scientific and Industrial Research, the Frank Smart Studentship for Research in Botany in the University of Cambridge, and a Caroline Turle Scholarship of Newnham College, Cambridge. A grant was also made by Newnham College toward the expenses of a visit to Leiden and Paris during March and April, 1955. Grateful acknowledgment is made for this support.

MORPHOLOGY AND DEVELOPMENT OF THE INFLORESCENCES

The morphology of the inflorescences in the genera under review has been studied by dissection and sectioning at anthesis and maturity and by examining different stages in the development where suitable material has been available. Material preserved in alcohol has been used as far as possible and has been supplemented by dried inflorescences, expanded by boiling in water, which can be quite suitable for study if they have been dried quickly (being sliced if they are at all large) and protected from insect attack. The development has not been studied previously except for brief observations on cultivated species of *Artocarpus* published by Baillon (1863) and Subba Rao (1940), which will be commented on below.

The arrangement of the inflorescence in the Urticaceae and Moraceae has been established as basically cymose by Bernbeck (1932) who showed that the dorsiventral inflorescences found in this alliance originate in the suppression of apical growth in a mono- or dichasium, the appearance of the primordia of the flowers and their subtending bracts being delayed, so that they arise on a variously shaped cushion of tissue representing the compressed inflorescence axis, or receptacle. He was able to do this both by making comparative studies in one genus (e.g., *Urtica*) showing progressive reduction in the inflorescence, and by analysing the arrangement and order of origin of the primordia in genera exhibiting a dorsiventral inflorescence only. The moraceous genera which Bernbeck studied were *Dorstenia* and *Ficus*: in the former the dichasial arrangement of the earliest primordia on the flattened receptacle was clearly distinguishable, although later this became obscured by the simultaneous origin of many primordia, but in the latter, though the first bracts were arranged cymosely, the flower primordia all appeared almost simultaneously.

It has been observed in the present study that the inflorescence of *Artocarpus incisus* shows a similar degree of reduction, the flower primordia in both male and female heads arising almost simultaneously and in no discernible order. The same phenomenon had earlier been noted for *A. heterophyllus* (as *A. integrifolia*) by Subba Rao (1940) in a paper on the cytology and embryology of this species. In both these species interfloral bracts are lacking, but in others where they are present (e.g., *A. hispidus* and *A. gomezianus* ssp. *zeylanicus*) they arise and mature a little earlier than the flower primordia, though they bear no definite relation to the latter. In the less reduced inflorescence of *Treculia africana*, however, the sympodial arrangement of the first few interfloral bracts is evident. These bracts, like those of most species of *Artocarpus*, terminate in a peltate scale and at the apex of the inflorescence there is always one conspicuously large scale, with a few somewhat smaller ones arranged meridionally and the rest of the surface covered by scales of irregularly decreasing size.

The inflorescences of *Prainea* and *Artocarpus*, on the one hand, and of *Parartocarpus* and *Hullettia*, on the other, have, as has already been indicated, a fundamentally different structure and hence they will be considered independently in the following account. The structure of the inflorescences is illustrated in *figs. 1–4*,[4] the species having been chosen both because they were typical and because, in *Artocarpus hispidus* and *Parartocarpus forbesii*, inflorescences preserved in alcohol were available.

In both male and female inflorescences of *Prainea* the perianths are tubular and free from each other, and are mixed with peltate to spathulate, long-stalked interfloral bracts. The male perianth is perforate or bilobed above and the apex of the female perianth is thick-walled and clavate, with a contracted mouth which is either perforate or very shortly 2–4-lobed. The female inflorescence of *P. papuana* is illustrated in *fig. 1, a–e* and the male inflorescence in *fig. 3, a–c*. As the female inflorescence ripens only

[4] For convenience of reference the figures will be numbered consecutively throughout this series of papers.

those perianths in which seeds are formed enlarge markedly. These become fleshy and appear as conical to globose projections from the general surface of the inflorescence, which is formed by the apices of the unexpanded flowers and the heads of the bracts, giving the typical appearance shown in *fig. 1, c.* Beccari (1902), in recognizing the affinities of *Prainea* with *Artocarpus,* stated that the only difference between the genera lay in the structure of the female inflorescence, but this is only correct with respect to the reproductive organs.

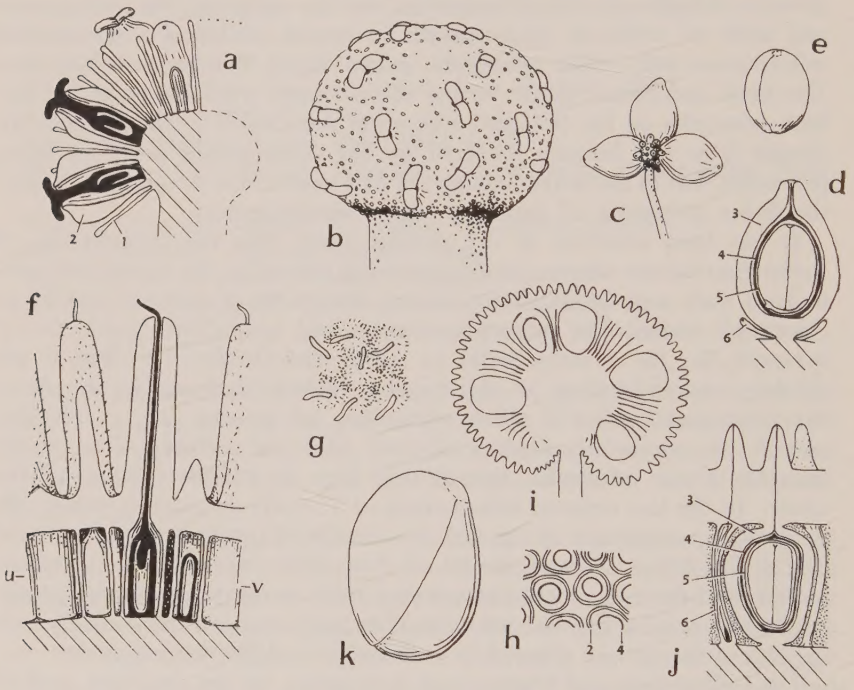

FIG. 1. The female inflorescence in *Prainea* and *Artocarpus.* a–e, *Prainea papuana*: a, b, longitudinal section and entire head at anthesis (× 5); c, mature head (× ½); d, fruiting perianth in longitudinal section (× 1); e, embryo (× 1). f–j, *Artocarpus hispidus*: f–h, longitudinal section, surface view and tangential section in plane u–v at anthesis (× 10); i, longitudinal section at maturity (× ½); j, part of the same (× 1). k, *A. incisus*, embryo (× 1).

Conventions used in *figs. 1–3*: ovaries and stamens are shown in black and receptacular tissue is crosshatched when cut in section. Abbreviations: 1, interfloral bract; 2, perianth; 3, fruiting perianth; 4, ovary; 5, testa; 6, unexpanded perianth; 7, involucral bract.

In the inflorescences of *Artocarpus* the flowers are also usually mixed with interfloral bracts, but these are frequently shed from the syncarp at or before anthesis and in some species they are altogether lacking. The perianths in the male inflorescence are likewise free from each other, varying from tubular to 2–4-partite, but in the female inflorescence the peri-

anths, which are tubular with a contracted and perforate apex, are fused with each other to form the characteristic syncarp from an early stage in development. This fusion is, however, only partial in most species and is of an unusual nature. Each perianth consists of a proximal region which is thin-walled and encloses the ovary, and a distal region with thickened walls and a narrow lumen through which the style passes to the exterior. Proximally the perianths remain free from each other, but distally they are connate, forming a continuous layer evidently capable of withstanding a considerable degree of tension as the syncarp matures. The perianths may

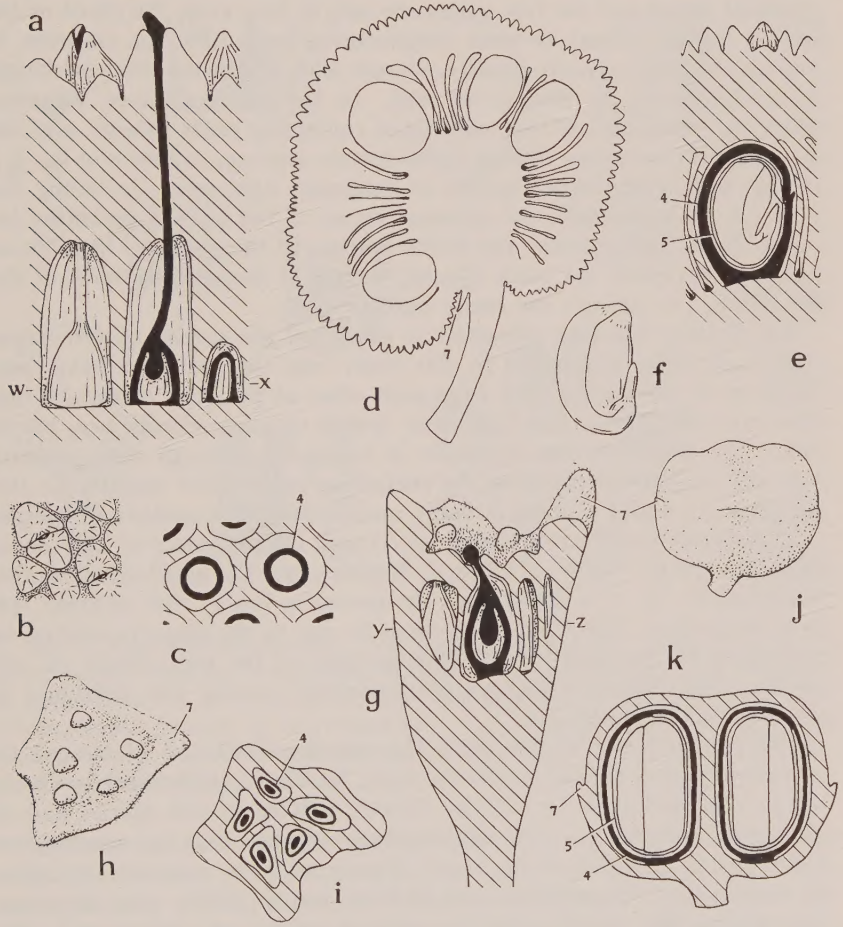

FIG. 2. The female inflorescence in *Parartocarpus* and *Hullettia*. a–f, *Parartocarpus forbesii*: a–c, longitudinal section, surface view and tangential section in plane w–x at anthesis (× 5); d, longitudinal section at maturity (× ½); e, part of the same (× 1); f, embryo (× 1). g–k, *Hullettia dumosa*: g–i, longitudinal section, surface view and tangential section in plane y–z at anthesis (× 5); j, mature head (× ½); k, the same in longitudinal section (× 1, approx.).

be completely fused distally to form a smooth covering layer to the syncarp with perforations through which the styles are exserted at anthesis, or their apices may remain free and project as cylindric, conical or obtuse processes on the surface. In *Artocarpus* (subg. *Artocarpus*) *hispidus*, which is illustrated in *fig. 1, f–j*, the distal parts of the perianths are not completely fused to each other and the syncarp is echinate from their rigid, free apices. The longitudinal section of the female inflorescence at anthesis in *fig. 1, f* shows one perianth cut sagittally, while those on either side are cut in a tangential plane, and in those on the extreme right and left the proximal region and the free apices are seen in face view, the plane of the section having passed between neighbouring perianths. In contrast to *Prainea* the entire syncarp usually enlarges more or less uniformly although relatively few of the flowers set seed. In the proximal layer, however, where the perianths are free, only those containing seeds enlarge, and the others appear as narrow ribbons in the mature syncarp, as shown in *fig. 1, j*. In this and several other species of subgenus *Artocarpus*, including the Jack (*A. heterophyllus*), the proximal region of the fruiting perianths becomes fleshy and provides the edible portion of the syncarp, in addition to the seeds, which are often roasted, though in the seedless form of the Breadfruit (*A. incisus*) the entire head is eaten.

The syncarp has been examined in nearly all the species of *Artocarpus* subg. *Artocarpus* recognized in this study and the perianths have been found to be consistently free from each other at the level of the ovaries. The same structure is found in many species of subg. *Pseudojaca*, but in others the fusion between perianths is complete, although each perianth may still be distinguishable on the surface as an areole or papilla. In this subgenus the entire syncarp is fleshy and is eaten in a number of species.

It has been possible to examine very young inflorescences of *Artocarpus rigidus*, a species closely allied to *A. hispidus*, and the longitudinal section illustrated in *fig. 4, a* shows that the perianths are at first entirely free from each other. The later fusion must be due to the pressure exerted on each other by the thick-walled distal portions of the very closely set primordia. The thinner-walled proximal portions, having less resistance to pressure, would remain free.

The partial fusion of the perianths was described and illustrated for *Artocarpus heterophyllus* (under the name *Sitodium cauliflorum*) by Gaertner in 1788 and again in 1939 by Corner, writing on this species and on *Artocarpus integer*, but other authors have assumed that the ovaries were embedded in a solid mass of tissue. Nearly all have regarded this tissue as representing the perianths, but Baillon, stated (1863) that the tissue surrounding the ovaries must be axial in origin, on the grounds that the belated fusion of neighbouring parts is very rare, as is indeed the case. He was able to study material of *Artocarpus incisus* preserved in alcohol, but, nevertheless, observing the very young pistils each in the centre of a ring-like emergence, he described them as becoming gradually more deeply sunken in pits of the receptacle and failed to notice the more complex adult structure.

In *Prainea* the male and female inflorescences are more or less globose and are not always easily distinguishable before anthesis, but in *Artocarpus* there is a considerable range of variation especially in the male head, and the two sexes usually differ markedly in size and shape. In neither genus is there a clearly differentiated involucre, although there may be few sessile bracts similar to the interfloral bracts at the base of the head. In *Artocarpus* there may be a slight enlargement of the top of the peduncle and in *A. heterophyllus* this forms a distinct annulus.

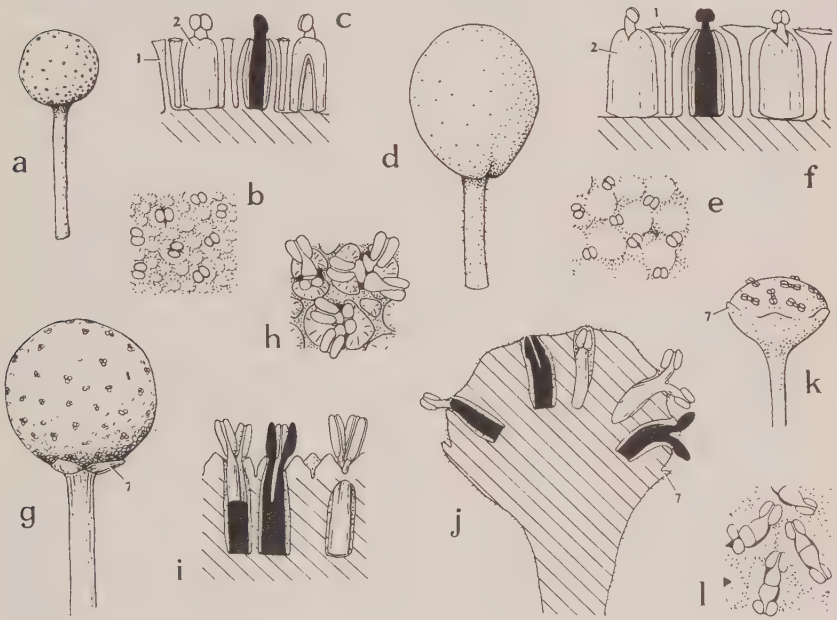

FIG. 3. The male inflorescence. a–c, *Prainea papuana*: a, entire head (× 1); b, c, surface view and longitudinal section (× 5). d–f, *Artocarpus hispidus*: d, entire head (× 1); e, f, surface view and longitudinal section (× 20). g–i, *Parartocarpus forbesii*: g, entire head (× 1); h, i, surface view and longitudinal section (× 5). j–l, *Hullettia griffithiana*: k, entire head (× 2); l, j, surface view and longitudinal section (× 5).

In *Parartocarpus* the inflorescences of the two sexes are similar to each other in structure, with both stamens and ovaries contained in cavities in the apparently continuous tissue of the capitula. Careful examination has revealed no sign of fusion having taken place between neighbouring perianths in the walls separating the cavities and developmental studies show that they are intercalary in origin. Details of the structure in *Parartocarpus forbesii* are shown for the female inflorescence in *fig. 2, a–f* and for the male inflorescence in *fig. 3, g–i*; comparison of the tangential section of the female inflorescence at the level of the ovaries (*fig. 2, c*) with that of *Artocarpus hispidus* (*fig. 1, h*) will show the difference between the

syncarps of the genera. The surface of the receptacle in *Parartocarpus* is closely covered by indurated processes, which are acutely conical or spinous in *P. forbesii*. Some are arranged in groups of two to four around the openings of the cavities containing the stamens or ovaries, and are fused basally to each other around the opening. The rest, which are identical in appearance, are free from each other and cover the intervening surface, bearing no relation to a cavity. The processes surrounding the openings are fused to each other only at the base at anthesis, but, since they grow from below, the fusion becomes more marked during the ripening of the syncarp. In spite of its different origin, this syncarp is superficially very similar to that of some species of *Artocarpus* in which the perianth apices are indurated.

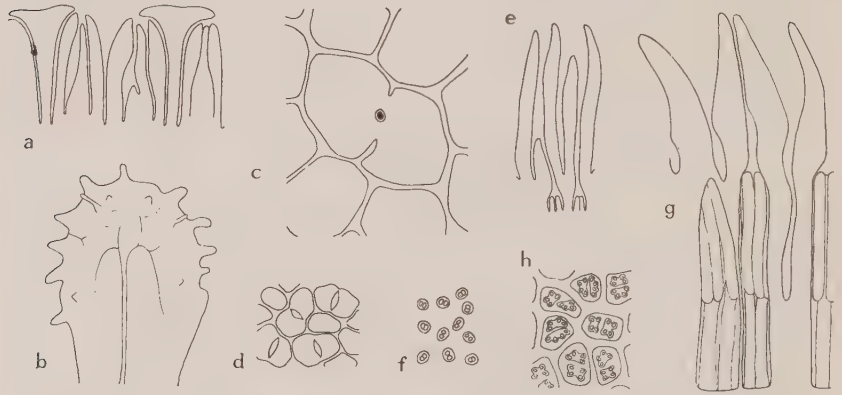

FIG. 4. Details of inflorescence structure. a, b, Longitudinal sections of young female inflorescences in *A. rigidus* (× 12.5) and *A. styracifolius* (× 2.5). c, d, Transverse sections through bases of perianths in female inflorescence of *Parartocarpus venenosus* at anthesis and in male inflorescence of *P. forbesii* before anthesis (× 5). e–h, Development of male head in *Parartocarpus bracteatus*: e, f, longitudinal and tangential sections from head 7 mm. in diameter (× 10); g, h, the same from head 25 mm. in diameter (× 5).

The development of the inflorescences is illustrated by the sections, both longitudinal and tangential at the level of the stamens, through male heads of *Parartocarpus bracteatus* in *fig. 4, e–h*. In this species the processes are spinous and the considerable enlargement of the cavities relative to the processes during their growth is evident on comparison of the figures. In the younger inflorescence (diameter of the head 7 mm.) the stamens are merely finger-like projections, while in the older one (diameter 25 mm.) they are nearly at anthesis. It has not been possible to examine any younger stage but it is probably justifiable to assume that the stamens arise between the processes on the surface of the receptacle and are only later enclosed within cavities. The intercalary origin of the walls is confirmed by the vertical lines of cells that are seen in longitudinal section. The processes are indurated from an early stage in development and can

therefore grow only at the base, while they must also enlarge laterally to cover the increasing surface area of the receptacle. It has not been possible to determine whether the processes surrounding each cavity are originally free, or whether they arise from a ring of tissue surrounding the androecium or gynoecium.

Varying opinions have been expressed as to the identity of the processes. In view of the similarity of the "fertile" and "sterile" processes it may be assumed that they are all equivalent; thus they presumably represent either perianths or interfloral bracts. Baillon, who was working with limited material of the male inflorescence, inaccurately stated in the original description of *Parartocarpus beccarianus* (1875) (= *P. venenosus* (Zoll. & Mor.) Becc.) that the stamens were intermingled with stalked bracts (the processes on the surface representing their heads), and hence supposed that the difference between this and the male inflorescence of *Artocarpus* lay in the absence of perianths. Boerlage (1897), who described the same species independently under the name *Gymnartocarpus venenosa* (based on *Artocarpus venenosa* Zollinger & Moritzi) likewise distinguished it from *Artocarpus* by the absence of perianths, but he described the stamens and ovaries correctly as sunken in cavities of the receptacle, regarding the processes alone as representing bracteoles. He failed to observe the fusion of the processes grouped around each cavity, which is not conspicuous in this species, since they are short and often truncate. The fusion is shown in the tangential section through the bases of the processes in *fig. 4, c.* Beccari, in discussing the inflorescence structure of *Artocarpus* and *Parartocarpus* in 1902, was the first to note the fusion of some of the processes in the latter. He considered that they represented the apical lobes of tubular perianths, which were completely fused to each other below, and that the free processes represented the solid apices of sterile perianths. While he realised that the processes thus differed from the tubular perforate perianth apices of *Artocarpus* he did not observe any difference in the internal structure.

Although the fusion of the processes around each cavity indicates that Beccari's interpretation is correct, apart from the fact that the tissue enclosing the stamens and ovaries is intercalary in origin and only the processes themselves can be regarded as representing the perianths (and even in these the base is also intercalary), the allied African genus *Treculia* must here be considered, since its less reduced condition may throw light on the structure of *Parartocarpus*.

In *Treculia africana*, well differentiated perianths, interfloral bracts and basal involucre are all present (illustrated in Engler, 1898, *t. 12–14*). The stalks of the abundant interfloral bracts are fused for about half their length, so that the flowers are enclosed in cavities between them. That this tissue represents the stalks of the bracts is shown by its continuity with the free distal portions of the stalks and the abrupt transition to receptacular tissue below the level of the flowers. In the male inflorescences the flowers consist of (2–)3–4(–5) stamens enclosed in a membranous tubular perianth. In the female inflorescence each ovary may be

accompanied by up to four linear perianth segments, and numerous abortive male flowers are also present. In this species each bract is terminated by a peltate scale, but in other species of the same genus the shape of the heads of the bracts is various. In *Treculia zenkeri* Engler (l.c., *t. 15*) the bracts have some peltate and some capitate heads, while in the male head of *Treculia obovoidea* N.E.Br. (as examined in *Zenker 2526*) the bracts terminate in minute spinous processes surrounding the cavities containing the flowers and bluntly conical processes covering the intervening surface. Hutchinson (1917) considered that *Acanthotreculia winkleri* Engler (1908) probably represented the female inflorescence of the latter species and in this the free spinous processes surrounding each emerging style were described as conspicuous and strongly differentiated from the other short and obtuse processes. The processes in both *Treculia zenkeri* and *T. obovoidea* have a general similarity to those on the surface of the inflorescences of *Parartocarpus* and the possibility must be considered that in the latter the bracts have secondarily assumed the function of perianth segments, those surrounding the openings of the receptacular cavities becoming partially fused to give added protection; that perianths containing the stamens and ovaries have been lost; and that walls of intercalary origin enclosing the latter have replaced the stalks of the now sessile bracts.

The inflorescence structure of *Hullettia* is fundamentally similar to that of *Parartocarpus*, although interfloral bracts and perianths are apparently entirely lacking and the fleshy, pubescent receptacle is naked, having perforations in the surface leading to cavities containing either stamens or ovaries. The female inflorescence of *Hullettia dumosa* is illustrated in *fig. 2, g–k* and the male inflorescence of *H. griffithiana* in *fig. 3, j–l*. No material has been available for studies in development, and the homology of the structure with that of *Parartocarpus* is inferred from examination of the inflorescences at anthesis and maturity and from other characters which the genera have in common.

The most immediately obvious of these similarities is that in *Hullettia*, as in *Parartocarpus* and *Treculia*, there is a clearly differentiated involucre. In *Parartocarpus* this consists of three to eight basal bracts which are triangular to ovate and indurated or thickly coriaceous. In *Hullettia* there are three to six fleshy flattened triangular projections which at anthesis are marginal on the obturbinate or pulvinate receptacle and on the subglobose mature syncarp vary from a basal to an equatorial position. In both genera the bracts may be somewhat obscured, especially on the mature syncarp of *Hullettia*. In *Parartocarpus* the inflorescences are globose or nearly so, like those of *Prainea*, and the male and female inflorescences can only be identified before anthesis by dissection, but in *Hullettia* it is only the very young inflorescences that are indistinguishable externally.

Details of the flowers have not been included in this discussion of the generic characters of the inflorescences, but those of the ovary will be considered in the following section. In *Prainea* and *Artocarpus* there is little variation in the male flowers and in distinguishing the species the entire inflorescence is the unit of variation. However, the male perianth

in *Artocarpus* subg. *Artocarpus* is nearly always tubular and bilobed above, whereas in subg. *Pseudojaca* it is frequently 2–4-partite, and, in the former, slight differences in the size of the anthers are of some assistance in establishing the subdivisions. There are also small differences in the stamens of the various species of *Parartocarpus* and *Hullettia*.

In conclusion, some aspects of the variability of the inflorescence within *Artocarpus*, which is in marked contrast to its relative uniformity within the other genera, will be commented on. In the syncarp, as in the male inflorescence, there is some overlapping in the characters of the two subgenera, so that they are most readily defined by the characters of the shoot. However, in subgenus *Pseudojaca* the syncarp is always more or less globose, with a surface varying from smooth to tuberculate, but never (except in *A. styracifolius*, discussed below) bearing distinctly elongate processes. In subgenus *Artocarpus*, on the other hand, the syncarp is always covered (at least at anthesis) by distinct processes, except in *A. sepicanus* and *A. kemando*, and in these, as in a majority of the other species, the syncarp is ellipsoid to cylindric.

The variety in the shape of the processes on the syncarp in *Artocarpus* subg. *Artocarpus* is considerable and will be illustrated in a plate accompanying the key to the subgenus. In a few species solid sterile perianths are present with elongate apices projecting markedly beyond those of the fertile perianths; in *A. multifidus*, *A. elasticus*, *A. sericicarpus* and *A. tamaran* the dimorphism is complete, but in *A. teysmannii* intermediates occur, all except the longest apices being perforate. This feature has either been unnoticed or its significance has been unrecognized by earlier authors. Elongate sterile perianths also occur in the male inflorescences of the first and last of these species. That these elongate processes represent sterile perianths and not enlarged interfloral bracts is shown by the finding of the latter in the same inflorescences, and by the close similarity of the perforate and solid processes in the syncarp.

In subgenus *Pseudojaca*, on the other hand, the flexuous, solid, terete processes that cover the surface of the syncarp of *A. styracifolius*, and between which the styles emerge through perforations in the surface, appear to be enlarged interfloral bracts. They have a single longitudinal vascular bundle, and in the young syncarp they look very similar to the clavate interfloral bracts found in the male inflorescence. A longitudinal section at this stage is shown in *Fig. 4, b*.

STRUCTURE OF THE SEED AND ITS GERMINATION

These genera are characterized by large seeds which have little or no endosperm and no period of dormancy or ability to withstand desiccation. Differences in the shape and orientation of the embryo and in the mode of germination confirm alliances indicated by the structure of the inflorescences. The ovule is pendulous at anthesis, being attached at or a little below the apex of the ovary, and the style is terminal or nearly so, but in the mature ovary the position of the style and the attachment of the seed

vary from apical to sub-basal, owing to differential growth in the walls of the ovary.

In *Prainea papuana*, the only species of the genus of which material was available for detailed study, the style is strictly terminal throughout, but, while at anthesis the ovule is attached laterally slightly below the apex of the ovary, at maturity it is sub-basal. The mature ovary is membranous and the testa is totally absorbed except for a thickened basal saucer-shaped region, at one side of which is the hilum. The embryo, which is illustrated in *fig. 1, e*, is symmetrical, with two equal cotyledons having their long axes parallel to the median plane of the ovary but their appressed faces at an angle of about 45° to it. The radicle and plumule are small and apical.

In *Artocarpus* there is great variation in the ovary and embryo and also in the consistency and relative thickness of the fruiting perianth, ovary and testa. In subgenus *Artocarpus* the terminal or lateral position of the style in the mature ovary delimits two natural groups of species. The seed is attached just below the base of the style and, since the radicle is usually directed approximately at the hilum, in the first group the embryo is longitudinally aligned and the radicle is apical, whereas in the second the long axis of the embryo is more or less oblique and the radicle is ventral. In the first group the appressed faces of the cotyledons are at an angle of 30–90° to the median plane of the ovary and the radicle and plumule are apical and minute so that the appearance of the embryo and its orientation relative to the ovary are similar to *Prainea*, although the hilum is apical instead of sub-basal. In these species the inner wall of the ovary forms a horny endocarp, while the exocarp decays leaving the "seed" free within the proximal region of the perianth which may be thickened and fleshy. In species in which the style is lateral or sub-basal in the mature ovary and the long axis of the embryo is hence more or less oblique, the appressed faces of the cotyledons may be in the median plane of the ovary (in which case the embryo is usually symmetrical), or they may also be oblique or at right angles to the median plane (in which case one cotyledon lies above the other in the seed and is frequently reduced in size). Such an embryo is illustrated in *fig. 1, k*. The variation in this second group will be discussed in more detail in considering the subdivision of subgenus *Artocarpus*. In this group the cotyledonary petioles and the radicle lying between them are relatively well developed and, if the latter is large enough, it is curved downward. The chalaza is always basal, with a conspicuous ventral raphe, so that in the first group the embryo is anatropous, whereas in the second it is campylotropous.

In *Artocarpus* subg. *Pseudojaca* the style is terminal or nearly so and the embryo is longitudinally aligned, with the appressed faces of the equal cotyledons in the median plane of the ovary or at varying angles to it. In some species of this subgenus, also, the seed is enclosed by an indurated endocarp which lies free in the cavity of the perianth at maturity.

The primary difference between the embryo in these genera and in *Parartocarpus* is that in the latter it is folded. The ovary has a terminal

style at anthesis, but at maturity it is lateral and the hilum lies just above it. The ovary wall differentiates into a bony endocarp and an exocarp which finally decays. The testa is attached to an indurated hilar plug and is thin-walled, with a relatively small apical vascular cap. The embryo fills it almost completely but, unlike *Artocarpus*, there are distinct remains of the endosperm in the region of the hilum. The markedly unequal cotyledons are appressed to each other and are incumbent, being folded transversely a little above the base so that the large, straight radicle lies along the median line of the inner and smaller cotyledon. The plane of the appressed faces of the cotyledons is longitudinal and at right angles to the median plane of the ovary. The tips of the cotyledons are enclosed in the vascular cap of the testa, which makes a distinct indentation in them, and the radicle lies on the side of the seed facing the style, its tip being directed upward to the hilum and enclosed in a pocket of endosperm. The embryo of *P. forbesii* is shown in *fig. 2, f*. The same type of embryo occurs in *Treculia* (*africana*) and has been illustrated by Trécul (1847) and Engler (1898) (but in *Acanthotreculia* Engler (1908) the embryo is shown with very unequal, straight cotyledons and a small, apical radicle).

The embryo of *Hullettia*, on the other hand, is straight, with equal or slightly unequal cotyledons arranged longitudinally; the small radicle, however, is basal. The ovary is pergamaceous and the testa has a shallow, thickened, apical cap (not shown in *fig. 2, k*) attached centrally, immediately below the subterminal style, and making an indentation in the tips of the cotyledons, but is otherwise thinly membranous. Thus, whereas in *Prainea* and *Artocarpus* the chalazal region is basal, in *Parartocarpus* and *Hullettia* it is apical (relative to the ovary), and since the tips of the cotyledons are in contact with this region, except in some species of *Artocarpus*, the orientation of the embryo with respect to the ovary is also reversed.

It has been possible to study germination in the following species of *Artocarpus*: (subg. *Artocarpus*) *A. rigidus*, *A. integer*, and *A. heterophyllus*, and (subg. *Pseudojaca*) *A. borneensis*. In addition I have been able to use Mr. Corner's notes on germination in *Artocarpus* (subg. *Artocarpus*) *anisophyllus*, *A. lanceifolius* and *A. elasticus* and *Parartocarpus bractcatus* and *P. forbesii*, and to examine herbarium specimens of seedlings of *Artocarpus incisus* and *A. nobilis*.

Germination in *Artocarpus* and *Parartocarpus* differs chiefly in whether or not there is elongation of the hypocotyl. In *Artocarpus* there is no elongation, and germination is hence hypogeal. The cotyledons usually remain enclosed within the testa and the plumule is enabled to emerge from between them by the elongation of their petioles (illustrated for *A. hirsutus* and *A. chaplasha* in Troup, 1921, *figs. 323, 325*). In *A. heterophyllus* (l.c., *fig. 324*, and Gaertner, 1788) and *A. integer*, however, the cotyledons separate to allow the emergence of the plumule. A further variation occurs in subgenus *Artocarpus* in the nature and arrangement of the first leaves borne by the seedling. The first pair subsequent to the seed leaves may be opposite and fully developed and be followed by spirally

arranged leaves (*A. anisophyllus*, *A. lanceifolius*, *A. rigidus*, *A. chaplasha*, *A. hirsutus* and *A. nobilis*) or the leaves may be spirally arranged from the first, the youngest being scale leaves (*A. incisus*, *A. heterophyllus*, *A. integer* and *A. elasticus*). The two types correspond, but only approximately, to the species groups distinguished above by the terminal and lateral position, respectively, of the style, and will likewise be discussed in more detail under subgenus *Artocarpus*. In *Artocarpus* subg. *Pseudojaca* the seedling bears scale leaves before the fully developed leaves, as in the second group above, but in *Artocarpus borneensis* (ssp. *griffithii*) these are strictly alternate and distichous from the first. It is not clear from Troup's illustration (l.c., *fig. 326*) of *A. lakoocha* whether the leaves are spirally or distichously arranged. Photographs of seedlings of *A. rigidus* and *A. borneensis* are reproduced in *fig. 5*.

In *Parartocarpus* germination is epigeal and the hypocotyl elongates markedly, carrying the folded cotyledons well above the ground. As they straighten and open out, becoming green and photosynthetic, the endocarp and testa are split off. The plumule grows out from between them and the first pair of leaves is opposite, with paired stipules, but the later leaves are spirally arranged, each with a single stipule. The seedlings of *Treculia africana* show an exactly similar mode of germinaton.

MORPHOLOGY OF THE SHOOT

The morphological characters of the shoot which are of importance in distinguishing the genera under review are principally those provided by the arrangement of the leaves and by the stipules, which enclose the terminal bud and are either intrapetiolar or lateral to the base of the petiole, being paired except in *Parartocarpus*. They are illustrated in *fig. 6*. It is in these characters that the most easily discernible distinctions are to be found between the two subgenera of *Artocarpus*. In subg. *Artocarpus* the leaves are spirally arranged and the stipules are intrapetiolar and amplexicaul, leaving annulate scars, whereas in subg. *Pseudojaca* the leaves are strictly alternate and distichous and the stipules are non-amplexicaul, leaving lateral or partially intrapetiolar scars. The latter arrangement is also found in *Prainea* but the leaves of this genus can usually be recognized by the abruptly and narrowly acuminate apex and the conspicuous and regular inarching of the lateral veins (in addition to details of the anatomy). In *Parartocarpus* the leaves are spirally arranged and in the axil of each is a single non-amplexicaul stipule which forms a scar extending slightly to either side of the petiolar scar. J. J. Smith (1922) was the first author to realize that these stipules were single and not paired. In the seedling, as already mentioned, they may be paired or have a bifid apex, indicating that each has originated from two stipules fused along their intrapetiolar margins. The leaf arrangement, together with the non-amplexicaul stipular scars, distinguishes the genus from both the preceding ones. The leaves of *Hullettia* are also spirally arranged but the stipules

FIG. 5. Seedlings of *Artocarpus*; left, *Artocarpus* (subg. *Artocarpus*) *rigidus*; right, *Artocarpus* (subg. *Pseudojaca*) *borneensis*; insets, details of stipules.

are distinctive, being linear, acute and frequently persistent. They are lateral to the leaf-axils and the scars are small and round.

Differences in the arrangement of the foliage are associated with the two types of phyllotaxy. In the groups with spirally arranged leaves the ultimate shoots and usually also the main branches are ascending. In *Parartocarpus* and *Hullettia* the leaves are markedly clustered at the tips of the shoots and there is greater elongation of the internodes at the base of each lateral branch, so that one leaf cluster is separated from the next.

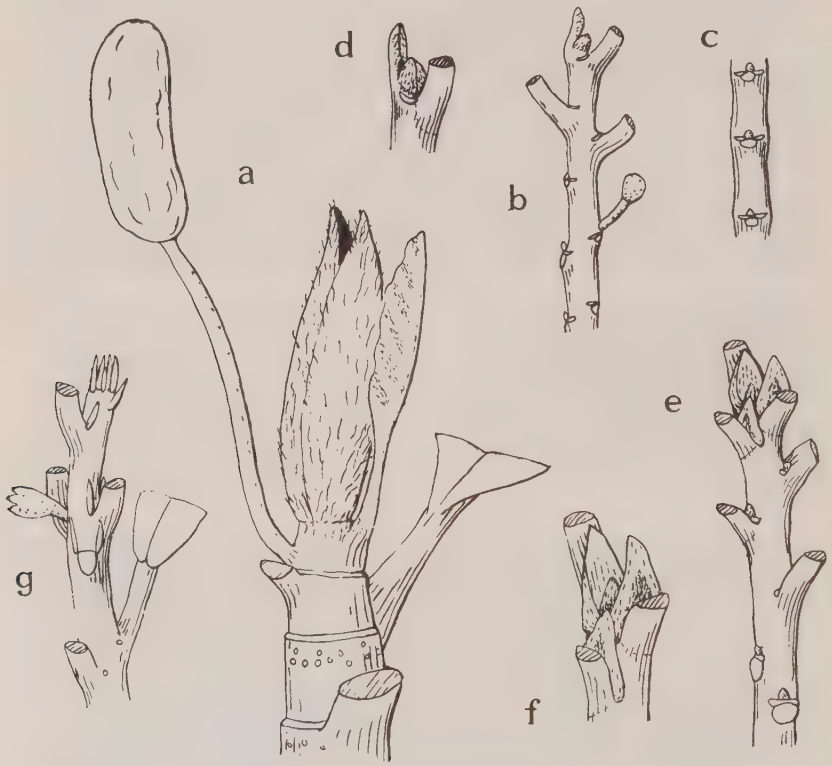

FIG. 6. Details of stipules; a, *Artocarpus sericicarpus* (× 1); b, c, *A. gomezianus* ssp. *zeylanicus* (× 1); d, terminal bud of the same (× 2); e, *Parartocarpus bracteatus* (× 1), f, terminal bud of the same (× 2); g, *Hullettia dumosa* (× 1).

In the groups with alternate leaves, on the other hand, at least the ultimate shoots are more or less applanate. As already mentioned, study of the seedlings of species belonging to both subgenera of *Artocarpus* has shown that the difference in leaf arrangement may exist from the earliest stage.

Leaf form in *Artocarpus* is variable, ranging from simple to pinnatifid. In most species the adult leaf is simple, but in one group within subg.

Artocarpus it is frequently pinnatifid, while in another species, *A. anisophyllus*, it is pinnate. In many other species of this subgenus the juvenile leaves are more or less pinnatifid and sometimes very large — to six feet in length in *A. elasticus* (Corner, 1940). *Artocarpus tamaran* is remarkable in having a nearly pinnate juvenile leaf, distinguished from that of *A. anisophyllus* by a continuous wing of lamina along the rachis. In some species of subg. *Pseudojaca* the juvenile leaves are irregularly pinnatifid or the lamina may be reduced to a sinuous wing along the midrib, but in the rest, as in the other genera, the leaf is always entire and the juvenile leaf is merely elongate. Juvenile leaf-forms are shown in *fig. 7*. As noted by Corner (1940) the pinnate leaves of *Artocarpus anisophyllus* are unusual in falling as a whole instead of disarticulating at the base of each pinna.

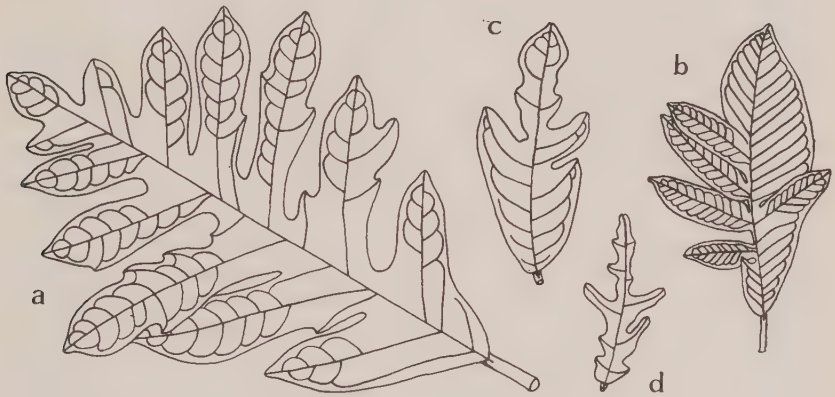

FIG. 7. Juvenile leaves in *Artocarpus*; a, *A. odoratissimus*; b, *A. tamaran*; c, d, *A. dadah* (× 1/7).

In the field *Artocarpus* and *Parartocarpus* are easily distinguished by characters of the bark. In *Artocarpus* the bark on the roots is red and that on the trunk peels off in flakes. In *Parartocarpus* the bark of the roots is yellow, while the trunk is covered by numerous large and prominent lenticels (conspicuous in the photograph in Browne, 1955).

LEAF ANATOMY

A detailed account of the leaf anatomy of the Artocarpoideae and Conocephaloideae was published by Renner in 1907. From this it may be concluded that the most important anatomical characters distinguishing the genera under consideration are those of the microscopic glandular epidermal hairs and of the spongy mesophyll. Renner considered that the fact that leaf anatomy of *Prainea* was in some ways intermediate to that of the two subgenera of *Artocarpus* necessitated the unification of the two genera, but this view is here rejected as a misinterpretation of the vegetative characters.

Renner's observations have been repeated in the course of this revision and expanded to cover all the species here recognized. They have in general been confirmed, but in the following discussion a few points of disagreement are indicated. The leaves were examined by means of surface and transverse sections cut from fragments of herbarium specimens boiled up in water, or from material preserved in alcohol when available. The sections were mounted in a solution of polyvinyl alcohol and lactic acid (Metcalfe and Richardson, 1950).

In addition to normal epidermal hairs the Artocarpoideae have gland-hairs on or sunken into the surface of the leaf, with a unicellular stalk and a variously shaped head. Renner stated that he was unable to find any anatomical characters distinguishing the tribes of the Artocarpoideae, but this may have been due in part to the fact that some genera were misplaced or studied from misidentified specimens. However, the Old World genera of Artocarpeae do show a wide range of variation in the gland-hairs, especially within the genus *Artocarpus*.

In *Prainea* and *Artocarpus* subg. *Artocarpus* the heads of the gland-hairs are 4–16-celled with a thick-walled stalk. In the former they are always and in the latter they are frequently sunken in pits in the epidermis. In *Prainea* the heads are depressed-globose and divided by vertical and horizontal walls into four to eight cells. In *Artocarpus* subg. *Artocarpus* the heads are either globose or depressed-globose with one or two tiers (rarely four) of four to six cells, or they are flattened and peltate with eight or rarely sixteen cells. An account of the gland-hairs is included in each specific description for this subgenus. In several species there is a hypodermis of cells which are either isodiametric or elongate in surface view. Both the gland-hairs and the hypodermis provide characters of taxonomic value and will be discussed further in considering the classification of the species of the subgenus.

In most species of *Artocarpus* subg. *Pseudojaca*, on the other hand, the gland-hairs have a unicellular globose head and a thin-walled stalk. Renner found the head to be 2–4-celled in *Artocarpus lakoocha* and in this study it also has been found to be 1–6-celled in *A. tonkinensis*. The gland-hairs of *Parartocarpus* likewise have a thin-walled stalk and a unicellular head, but the latter is markedly elongate and thus cylindric. In *Hullettia*, which was omitted by Renner as being of doubtful affinities, the gland-hairs have a thick-walled stalk and a globose unicellular head. According to Renner the gland-hairs of *Treculia* have an elongate head often divided by a longitudinal wall. In none of these are the gland-hairs sunken, except for a few species of *Artocarpus* subg. *Pseudojaca* in which they are only slightly so, and in none is there a hypodermis.

In the characters of the spongy mesophyll the two subgenera of *Artocarpus* again differ widely, while *Prainea* occupies a somewhat intermediate position. All the genera being studied have a bifacial leaf with one or two rows of palisade cells, and a well developed spongy mesophyll. This is more or less compact in *Artocarpus* subg. *Pseudojaca*, *Parartocarpus* and *Hullettia*, but in *Artocarpus* subg. *Artocarpus* it is extremely loose, consisting

of a mesh of long-armed ("hyphenartig") cells and including some conspicuous ellipsoid or globose cells with resinous contents. The resin cells are absent in *A. heterophyllus* and *A. integer*, but not, as stated by Renner, in *A. odoratissimus* (as *A. mutabilis* Becc.). In *Prainea* the spongy mesophyll is rather loose with relatively large cells nearly all having slightly resinous contents.

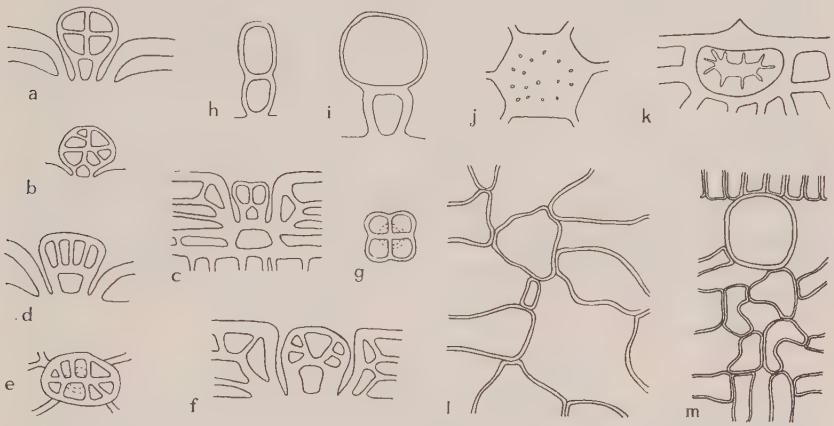

FIG. 8. Details of leaf anatomy. a–i, Epidermal glands: a–c, *Prainea limpato*, *Artocarpus odoratissimus* and *A. lanceifolius* in longitudinal section (the last also showing hypodermis); d, e, *A. treculianus* in longitudinal section and surface view; f, *A. integer* in longitudinal section; g, *A. sericicarpus* in surface view; h, i, *Parartocarpus venenosus* and *Hullettia dumosa* in longitudinal section. j, k. Enlarged epidermal cells in *Hullettia dumosa* in surface view and longitudinal section. l, m, Spongy mesophyll in *Prainea frutescens* and *Artocarpus rigidus* in longitudinal section (the latter showing resin cell in contact with palisade tissue) (× 200, approx.).

On the grounds that, firstly, *Prainea* showed more similarity in anatomical structure to *Artocarpus* subg. *Artocarpus* than the latter did to subg. *Pseudojaca,* and that, secondly, according to Beccari (1902) the only difference between the genera lay in the free or fused female perianths, Renner treated all three groups as sections under *Artocarpus*. However, the mesophyll of *Prainea* could well be regarded as a type from which the two subgenera of *Artocarpus* have diverged, while subg. *Artocarpus* and subg. *Pseudojaca* may show an advance and a reduction respectively in the development of the gland-hairs. In leaf and stipular arrangement *Prainea* resembles *Artocarpus* subg. *Pseudojaca*. The interrelations between the three groups thus appear reticulate, indicating that parallel evolution has occurred. This is least likely to have occurred in the unique sycarpium of *Artocarpus* and most probable in the development of distichous leaves and non-amplexicaul stipules. It is therefore concluded that *Prainea* and *Artocarpus* should be retained as distinct genera and that the anatomical characters of the latter have probably arisen

by divergence from a common ancestor with *Prainea*. The anatomical characters, in conjunction with the difference in leaf and stipular arrangement, provide the best evidence that the subgenera of *Artocarpus* represent natural groups.

In their indumentum (apart from the gland-hairs) all the genera are variable, except for *Prainea*, in which the leaves are glabrous. The hairs frequently have enlarged bases and papillate walls, though, as was noted by Renner, there may be a few hairs with hooked tips and these are always smooth walled. In *Prainea* there are likewise enlarged cells in the epidermis which may be produced into a very short point. In *Artocarpus* the hairs are usually restricted to the veins, but in some species of subg. *Pseudojaca* nearly all the cells of the areolae grow out to form thin-walled, often crisped hairs, so that the lower surface appears greyish-glaucous from the minute tomentum. In *Hullettia* there are numerous enlarged cells with strongly thickened and narrowly pitted walls in the lower epidermis, which bear hairs of varying length and cause the lower surface to appear minutely punctate under a lens.

GENERAL CONCLUSIONS

The conclusions reached in the foregoing discussion are summarized below in the order in which the characters were taken up.

The inflorescences of *Prainea* and *Artocarpus* are covered by well developed perianths enclosing the stamens and ovaries and mixed with interfloral bracts, but they lack a clearly differentiated involucre. In the female inflorescence of *Artocarpus* the perianths are fused to form a syncarpium. Dissection shows that the proximal portions of the perianths, enclosing the ovaries, usually remain free, while the distal portions fuse, either completely or leaving the apices free, to form an external wall. The perianths have been found to be completely free in the very young inflorescence. In some species (in subg. *Pseudojaca*) the fusion between the perianths is complete, but it is assumed that the structure of the syncarp is homologous.

In *Parartocarpus* the stamens and ovaries are sunken in cavities which are described as receptacular, and have been shown to be separated by walls that are largely if not entirely of intercalary origin. The surface of the receptacle is covered by indurated, spinous, conical or truncate processes that may represent either perianth segments fused basally around the opening of each cavity and solid sterile perianths between these, or secondarily modified interfloral bracts, taking into account the less reduced structure of the related African genus *Treculia*. In *Treculia* perianths are present (tubular in the male, and of linear segments in the female) and are sunken with the stamens of ovaries between the fused stalks of interfloral bracts, the heads of which somewhat resemble the processes in *Parartocarpus*. In both these genera there is a well developed basal involucre. The ovule has been found to be pendulous rather than basal in *Hullettia* and the genus is therefore removed from the Conocephaloideae to the Arto-

carpoideae. The stamens and ovaries are apparently enclosed in cavities as in *Pararartocarpus* and there is an involucre of fleshy bracts. It is assumed that the structure of the receptacle is homologous, and that the surface is naked, perianths and interfloral bracts being absent.

The orientation of the embryo and the mode of germination confirm the above alliances. In *Prainea* and *Artocarpus* the embryo is straight (or nearly so) and germination in the latter is hypogeal. In *Pararartocarpus* and *Treculia* the embryo is curved, with folded incumbent cotyledons, and germination is epigeal. The embryo of *Hullettia* resembles that of *Pararartocarpus* in its orientation but is straight.

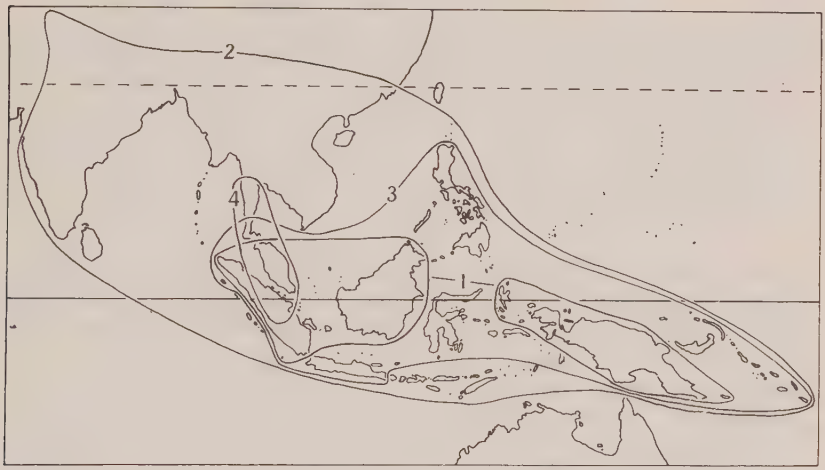

FIG. 9. Distribution of the genera. 1, *Prainea*; 2, *Artocarpus*; 3, *Pararartocarpus*; 4, *Hullettia*.

The arrangement of the leaves and stipules serves to distinguish *Pararartocarpus* and *Hullettia* from each other, and also from *Prainea* and *Artocarpus*. In the last genus this character readily defines two natural subgenera, *Artocarpus* and *Pseudojaca*, further differentiated by details of the glandular epidermal hairs and the spongy mesophyll which also separate them from *Prainea*. Renner's observations (1907) on leaf anatomy have been expanded and confirmed but his reduction of *Prainea* to the status of a section under *Artocarpus* is not upheld. In vegetative characters the interrelations between the three groups are reticulate, but these indicate the occurrence of parallel evolution and the differences in the female inflorescences override them.

Prainea, Artocarpus, Pararartocarpus and *Hullettia*, together with *Treculia*, form a group of genera united by their condensed capitate inflorescences and large embryos. *Prainea* and *Artocarpus* are closely related to each other, while *Treculia*, *Pararartocarpus* and *Hullettia* form a less closely allied series, both groups showing increasing reduction of the inflorescences. Whether these genera together form a natural group within

the Moraceae cannot be certain until an up-to-date revision of the entire family has been carried out, but, from a review of the other Old World genera, it seems probable. The syncarpia of *Artocarpus* and *Parartocarpus* are striking examples of parallel evolution. These two genera and *Hullettia* each represent a highly specialized evolutionary end-point, though reflecting a general tendency for the female inflorescence to become a syncarpium having the ovaries enclosed in either floral or axial tissue.

KEYS TO THE OLD WORLD GENERA OF THE ARTOCARPEAE

Natural Key

1. Inflorescences without an involucre; embryo straight.
   2. Female perianths free, only fruiting perianths enlarging and projecting beyond surface of mature head; leaves alternate and distichous; stipules and scars lateral or partially intrapetiolar; gland-hairs with 4–8-celled head; mesophyll loose, cell-contents resinous. ..... 1. *Prainea.*
   2. Female perianths fused to form a syncarp; entire head enlarging at maturity. ..... 2. *Artocarpus.*
      3. Leaves spirally arranged; stipules amplexicaul, scars annulate; gland-hairs with 4–16-celled head; mesophyll long-armed with globose or ellipsoid resin-cells. ..... Subgenus *Artocarpus.*
      3. Leaves alternate and distichous; stipules and scars lateral or partially intrapetiolar; gland-hairs with 1(–6)-celled head; mesophyll compact, lacking resin-cells. ..... Subgenus *Pseudojaca.*
1. Inflorescences with an involucre of triangular, ovate or orbicular bracts; embryo curved (except *Hullettia*).
   4. Involucre multiseriate; stamens enclosed in tubular perianths, these and ovaries sunken between partially fused interfloral bracts; stipules amplexicaul, scars annulate. ..... (*Treculia*).
   4. Involucre uniseriate; stamens and ovaries sunken in cavities in receptacle; stipules non-amplexicaul, scars not annulate.
      5. Surface of receptacle armoured from indurated, spinous, conical or truncate processes; stipules fused, intrapetiolar, triangular. ..... 3. *Parartocarpus.*
      5. Surface of receptacle not armoured, smooth; stipules paired and lateral, linear. ..... 4. *Hullettia.*

Artificial Key based on Vegetative Characters

1. Stipules amplexicaul, leaving annulate scars.
   2. Leaves spirally arranged. ..... 2. *Artocarpus* subg. *Artocarpus.*
   2. Leaves, at least on ultimate branches, alternate and distichous. (*Treculia*).
1. Stipules not amplexicaul, scars not annulate.
   3. Leaves spirally arranged.
      4. Stipules paired, linear, scars lateral, round; leaves minutely punctate beneath. ..... 4. *Hullettia.*
      4. Stipules fused, intrapetiolar, scars elongate; leaves not as above. ..... 3. *Parartocarpus.*
   3. Leaves alternate and distichous.
      5. Leaves abruptly and distinctly acuminate, glabrous; gland-hairs sunken, head 4–8-celled; mesophyll loose, cell contents resinous. .. 1. *Prainea.*

5. Leaves usually not abruptly acuminate, often pubescent; gland-hairs not sunken, head 1(–6)-celled; mesophyll compact, without resin. ..... 2. *Artocarpus* subg. *Pseudojaca*.

NOTES ON THE TAXONOMIC TREATMENTS

Keys. These are intended to indicate, as far as is practicable, the natural affinities of the species and to enable the identification of most material bearing either male or female inflorescences and, where possible, of sterile specimens. Distinguishing characters for sterile material of species with overlapping areas of distribution have been given in the notes under the species.

Types. These have been listed, where known, at the end of the references for each accepted name and synonym. All these specimens have been examined unless otherwise stated. Detailed localities have been given here only when the type or a duplicate has not been seen, since they otherwise appear in the lists of specimens. Lectotypes have been selected for most species where the original description gave syntypes and for those species where the holotype has been destroyed, but isotypes exist. Neotypes have only been chosen, where necessary, for accepted names.

Specific descriptions. These have been prepared from herbarium material, with the addition of details from field notes. The inflorescences have been described from material preserved in alcohol when this has been available. Otherwise the male flowers have been described from material boiled up in water. Where measurements in published descriptions differ greatly from those found in the specimens seen they have been given, together with the source. Measurements of the female inflorescences are probably frequently too small, since fully ripe fruits are not often collected, and many of the species will certainly have larger sapling leaves than indicated here. Descriptions of new species have been prepared from the types and supplemented by details from other collections enclosed in brackets.

Details of the stipules have only been given for *Artocarpus* subg. *Artocarpus*, *Parartocarpus* and *Hullettia*, since in the other groups they do not show significant variation between the species. For the same reason, details of the glands on the leaves and of the presence or absence of a hypodermis have only been given for *Artocarpus* subg. *Artocarpus*. In describing the leaves the term "main veins" includes the midrib and the lateral veins, while the term "reticulum" includes the intercostals unless these have been mentioned separately. In counting the lateral veins all those at the base have been included as well as all those clearly distinguishable at the apex.

The inflorescences have been described as immature before anthesis and the female inflorescence has been described as submature between anthesis and maturity. In *Prainea* and *Artocarpus* the interfloral bracts (as opposed to the involucral bracts of *Parartocarpus* and *Hullettia*) are referred to as bracts in the descriptions. In describing the syncarp of *Artocarpus* and *Parartocarpus* the variously shaped projections of the

surface, excluding peltate interfloral bracts, are referred to as processes or papillae. The morphological nature of these, which has already been discussed, differs both within *Artocarpus* and between *Artocarpus* and *Parartocarpus*. The terms "core" and "wall" refer respectively to the receptacle and the surface layer formed by the fused perianths.

CITATION OF SPECIMENS. These have been listed by areas, arranged from west to east in continental Asia (excluding Malaya) and according to the enumeration of geographical units by van Steenis (1950) in Malaysia, except that in the latter the order of the first four units has been changed to Malaya, Sumatra, Borneo, Java, in order to reflect the geographical continuity of Malaya with Asia and the close connection of Borneo with Malaya and Sumatra. In the Philippine Islands, Luzon and Mindanao have been further subdivided into provinces, and specimens from eastern New Guinea have also been listed according to recent political subdivisions.

The herbaria in which the collections have been seen are indicated by the abbreviations of the Index Herbariorum, Part I. ed. 3. 1956. These have been given above in conjunction with the acknowledgements. In addition, the following abbreviations may be noted which have been used preceding the collection numbers.

bb — Bossen buitengewesten; i.e., collections made by the Netherlands Indies Forest Service from areas outside Java.
BS — Bureau of Science, Manila, Philippines.
CF — Conservator of Forests series, Forest Institute, Kepong, Malaya.
FB — Forestry Bureau, Manila, Philippines.
NIFS — Netherlands Indies Forest Service; this has been prefixed to those collections made by the service which do not have bb numbers. (They are numbered in several series, distinguished by various abbreviations indicating where they were collected.)
PB — Piante Bornensi; collected by Beccari.
PP — Piante Papuane; collected by Beccari.
SB — Species Blancoanae; collected by Merrill to illustrate his book of that title.
SFN — Singapore field number.

Localities have been cited as given on the original label, apart from some minor corrections. Where important alterations have been necessary, these have been added in brackets. The Dutch *oe* has been transliterated throughout as *u*. The presence of male and female inflorescences has been indicated, but in *Prainea, Parartocarpus* and *Hullettia* the sex of immature inflorescences can often be determined only by dissection, and these have been recorded as "infl."

VERNACULAR NAMES. Only those names have been cited which are of fairly common occurrence for a given species, or which are of particular interest. The following names are applied to any species of *Artocarpus* subg. *Pseudojaca*: *Chay* or *Cay chay* (Annamite), *Kwai muk* or *Hung kwai muk* (China), *Tampang* (Malay), and *Cubi* and *Anubing* (Philippines). The name *Tampang* is also applied to *Prainea limpato*. In *Artocarpus* subg. *Artocarpus*, *Terap* is the Malay name for *A. odoratissimus*, *A. scorte-*

chinii, *A. elasticus*, *A. sericicarpus* and *A. tamaran*. Many other species of this subgenus are distinguished by their own names, which are usually accurately applied.

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STUDIES IN ARTOCARPUS AND ALLIED GENERA, II. A REVISION OF PRAINEA

FRANCES M. JARRETT

Prainea King in Hook. f. Fl. Brit. Ind. **5**: 546. 1888; King, Ann. Bot. Gard. Calcutta **5**(2): 162. *t. 196.* 1896; Engler & Prantl, Nat. Pflanzenfam. Nachträge II–IV. 122. 1897; Boerl. Handl. Fl. Ned. Ind. **3**: 337, 372. 1900; Becc. For. Borneo 635. 1902, Webbia **5**: 563. 1923; Ridley, Fl. Malay Penin. **3**: 358. 1924; Van Steenis, Bull. Jard. Bot. Buitenzorg III. **12**: 259. 1932; Jarrett, Jour. Arnold Arb. **40**: 8, 11. *fig. 1, a–e, fig. 3, a–c.* 1959. TYPE SPECIES: *Prainea scandens* King.

Artocarpus section *Prainea* Renner, Bot. Jahrb. **39**: 366. 1907.

Trees (? or climbers). *Leaves* alternate and distichous, simple, entire, penninerved, glabrous; epidermal gland-hairs sunken, heads globose, 4–8-celled; spongy mesophyll loose, cell contents somewhat resinous; juvenile leaves elongate. *Stipules* paired, small (to 5 mm. long), lateral or intrapetiolar, scars non-amplexicaul.

Inflorescences unisexual, capitate, heads globose, or the male short-obovoid, pedunculate, solitary or paired in leaf-axils; flowers mixed with numerous narrowly peltate, clavate or spathulate interfloral bracts; perianths free, enclosing a single stamen or ovary; involucre absent. *At anthesis* perianths and bracts compactly covering surface; *male head* with numerous flowers; perianths tubular, bilobed or perforate above; stamens shortly exserted; *female head* with fewer flowers (c. 20–100); perianths tubular, clavate, fleshy above, the mouth contracted, very shortly 2–4-lobed or merely perforate; ovary unilocular, style apical, bifid, the branches exserted, ovule subapical. *Mature female head* with 1–20 flowers forming fruit, perianths greatly enlarged and projecting from surface, fleshy, subglobose to ellipsoid; remaining perianths elongating somewhat or not at all and surface hence loose or compact; mature ovary membranous, style apical, seed large, attached laterally near base, testa absorbed except the thickened saucer-shaped basal portion, endosperm none, embryo straight, longitudinal, cotyledons equal, appressed faces oblique to median plane of ovary, radicle and plumule minute, apical; interfloral bracts persistent.

DISTRIBUTION: Malaya, Sumatra, Borneo, Moluccas, New Guinea.

The genus *Prainea*, described by King in 1888, was based on a single species from Malaya, *P. scandens*, which he illustrated in 1896 in "A Century of New and Rare Indian Plants." King described the ovule as basal and hence placed the genus incorrectly in the Conocephaloideae. However, although the mature seed is attached sub-basally (in *P. papuana*, the only species of which adequate material has been available for study),

if the ovary is examined at anthesis the position of the ovule is found to be lateral just below the apex of the loculus.

In 1902 Beccari, in the appendix to "Nelle Foreste di Borneo" entitled "Nuove Specie di *Artocarpeae* Malesi e Papuane," briefly discussed the inflorescences of *Prainea*, stating that he had found the ovule to be pendulous [at anthesis] in spirit material of his *P. cuspidata* (= *P. limpato*) and that the genus was allied to *Artocarpus*, differing only in the structure of the female inflorescence. He also questioned King's description of *Prainea scandens* as a climber. He described as new the three other species of *Prainea* here recognized and a fourth which was an identification of Rumphius' *Metrosideros spuria* (= *Artocarpus fretissii* Teysmann & Binnendijk).

FIG. 10. Distribution of the species of *Prainea*, with inset showing styles; 1, *P. scandens;* 2, *P. frutescens;* 3, *P. limpato;* 4, *P. papuana.*

Renner's reduction of the genus in 1907 to the status of a section under *Artocarpus* has been discussed fully in the introductory paper of this series and rejected on the grounds that the resemblance in leaf structure to subg. *Artocarpus* and in leaf and stipular arrangement to subg. *Pseudojaca* is of less significance than the difference between the free perianths of the female inflorescence of *Prainea* and the syncarpium of *Artocarpus*. In uniting *Prainea* with *Artocarpus,* Renner correctly identified Beccari's *Prainea cuspidata* with Miquel's *Artocarpus limpato* (1861) and listed four species which are equivalent to those recognized here. He found the ovule to be pendulous in *Prainea frutescens* and thus the only species in which this character has not been established is *P. scandens.*

The species are readily separable and the characters used may be seen from the key. No marked variation occurs within the genus, although *P. scandens* and *P. frutescens*, on the one hand, and *P. limpato* and *P. papuana*, on the other, are somewhat more closely allied to each other by leaf characters and the length of the peduncle.

The genus *Prainea* is entirely restricted to Malaysia, with three species in western Malaysia, of which one is endemic to Malaya, and another to Borneo, and a single species in the Moluccas and New Guinea. Van Steenis, in discussing the distribution of the Styracaceae in 1932, cited *Prainea* as an example of a genus which, like that family, occurs in both the western and the eastern parts of Malaysia, but not in the Philippines. The absence of *Prainea* from the Philippines has been confirmed thus far and, moreover, the genus is apparently lacking from nearly all of the geologically unstable area between the Sunda and Sahul continental shelves. Species of *Artocarpus* showing a similar pattern of distribution will be noted in a discussion of the geographical distribution of this group of genera at the conclusion of this series of papers.

KEY TO THE SPECIES OF PRAINEA

1. Male peduncles 5–15 mm.; female peduncles 10–25 mm.; twigs c. 1.5 mm. thick; leaves with 6–12 pairs lateral veins.
   2. Male heads to c. 15 mm. across; female heads to c. 35 mm. across with fruiting perianths projecting up to 25 mm.; stylar branches 2 mm. long, acute. ..... 1. *P. scandens.*
   2. Male heads 4–6 mm. across; female heads to c. 10 mm. across with fruiting perianths projecting less than 10 mm.; stylar branches 0.5 mm. long, truncate. ..... 2. *P. frutescens.*
1. Male peduncles 15–60 mm.; female peduncles 35–110 mm.; twigs 2–5 mm. thick; leaves with 9–24 pairs lateral veins.
   3. Male heads to c. 15 mm. across; female heads to c. 35 mm. across with fruiting perianths projecting up to 15 mm.; stylar branches forked; mature leaves with lateral veins distinctly prominent beneath, areolae bullate above only, or not at all. ..... 3. *P. limpato.*
   3. Male heads 3–8 mm. across; female heads to 20 mm. across with fruiting perianths projecting up to 10 mm.; stylar branches obtuse; mature leaves with lateral veins not or shallowly prominent beneath, areolae often bullate on both surfaces. ..... 4. *P. papuana.*

1. **Prainea scandens** King in Hook. f. Fl. Brit. Ind. **5**: 547. 1888; King, Ann. Bot. Gard. Calcutta **5**(2): 162. *t. 196.* 1896; Ridley, Fl. Malay Penin. **3**: 358. 1924. Syntypes, Malaya, *King 3549*, *3693* (CAL, not seen); duplicates examined (BM, K).

Artocarpus scandens Renner, Bot. Jahrb. **39**: 367. 1907.

Climber(?), height to 20 m. *Twigs* c. 1.5 mm. thick, finely rugose, minutely appressed pubescent, soon glabrescent. *Leaves* 9–17 × 3.5–7 cm., obovate-elliptic, varying elliptic or oblong-elliptic, abruptly contracted into a narrow acumen to 1.5 cm. long, base cuneate, margin entire; midrib prominent beneath, lateral veins slightly so; lateral veins 9–12 pairs, curved, inarching at margin, often with secondary loops; intercostals not parallel; glabrous, dark green, drying greenish above, pale to reddish brown beneath, petiole 5–15 mm. long.

Inflorescences solitary in leaf-axils. *Male head* (not at anthesis) to 15 mm. across, short-obovoid; perianths tubular, bilobed above, 1 mm. long; stamen immature, filament cylindric, anther oblong, 0.3 mm. long; bracts slenderly stalked, heads peltate, 0.4 mm. across; peduncle to 15 × 1.5 mm.. velutinous; *female head* at anthesis with bifid styles exserted, branches 2 × 0.2 mm., acute. *Mature female head* to 35 mm. across (excluding fruiting perianths), globose, loosely covered by numerous flowers and bracts, yellow, drying brown; fruiting perianths 1–7, projecting to 25 mm., ellipsoid, 15 mm. across, broadly and obtusely attenuate; remaining perianths 12–15 mm. long, apices clavate, perforate, minutely pubescent, 0.8 mm. across; bracts numerous, slenderly stalked, heads clavate, 0.8 mm. across, pubescent; peduncle 20–25 × 2.5 mm., puberulent.

Distribution: in lowland evergreen forest to 2500 ft., endemic to Malaya.

Malaya. Perak: Larut, *King 3549*, Nov. 1882 (BM, K, ♂), *King 3693* Dec. 1882 (BM, K, ♀). Selangor: bridge where Gap road crosses Sungei Semangko, *Strugnell Kepong FN 49703* (SING, ♀, detached inflorescence with leaves of *Artocarpus rigidus*).

The material of this species is inadequate, but King's collections agree well on vegetative characters and the mature female head on *Strugnell Kepong FN 49703* matches that of *King 3693*.

This species appears to differ from all others in *Prainea* and *Artocarpus* in being a climber instead of a tree. The labels on both King's collections describe the plants as "creepers." *King 3693* originally read "a tree with slender hanging branches 50–60 ft. high . . . clinging to another tree" and was altered later.

2. **Prainea frutescens** Becc. For. Borneo 635. 1902. Holotype, Borneo, *Beccari PB 667* (FI); isotypes (FI, K, P).

Pararartocarpus sp. Benth. & Hook. f. Gen. Pl. 3: 375. 1880.
Artocarpus frutescens Renner, Bot. Jahrb. 39: 367. 1907.

Trees, height to 30 m. *Twigs* c. 1.5 mm. thick, finely and acutely rugose, appressed puberulent, soon glabrescent. *Leaves* 5–16 × 3–7 cm., obovate-elliptic to obovate- or elliptic-oblong or elliptic, abruptly contracted into a narrow acumen to 2 cm. long, base cuneate, rarely oblique with one side rounded, margin entire; midrib prominent beneath, lateral veins slightly so; lateral veins 6–10 pairs, curved, inarching at margin; intercostals not parallel; glabrous, drying greenish to pale or reddish brown; petiole 7–12 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis*: *male head* 4–6 mm. across, subglobose to short-obovoid; perianths tubular, 0.8 mm. long, minutely pubescent; stamen 1.2 mm. long, filament cylindric, anther oblong, 0.15 mm. long; bracts slenderly stalked, heads peltate, 0.3 mm. across, ciliate; peduncle 5–12 × 1 mm., velutinous; *female head* with

bifid styles exserted, branches 0.6 × 0.2 mm., truncate. *Mature female head* to 10 mm. across (excluding fruiting perianths), globose, compactly covered by 20–30 flowers and numerous bracts; fruiting perianths 2 (in only mature head seen) projecting to 7 mm., ovoid, 6 mm. across, obtuse; remaining perianths c. 2.5 mm. long, apices obtuse, minutely pubescent, 1.5 mm. across, mouth shortly bilobed; bracts coherent in groups, slenderly stalked, heads narrowly peltate, 0.25 mm. across, pubescent; peduncle 13–16 × 1.5 mm., short-pubescent.

DISTRIBUTION: in lowland evergreen forest to 200 ft., endemic to Borneo.

Borneo. SARAWAK: near Kuching, *Beccari PB 667*, Nov. 1865 (FI, K, P, ♂, ♀), *Haviland 3111* (BM, BO, ♀). EAST AND NORTHEAST BORNEO. W. Kutei: *bb 16183* (A, BO); Longbleh, Sungei Pekan, *bb 29606* (A, BO, L, SING, ♂); Mujup, *bb 16785*, *bb 16911* (A, BO, L).

3. Prainea limpato (Miq.) Beumée ex Heyne, Nutt. Pl. Ned.-Ind. ed. 2. 1: 579. 1927.

Artocarpus limpato Miq. Fl. Ind. Bat. Suppl. 421. 1861; Renner, Bot. Jahrb. **39**: 367. 1907. Syntypes, Sumatra, *Diepenhorst HB 2092*, *HB 2500* (U); lectotype, *Diepenhorst HB 2092* (U).

Urostigma diepenhorstii Miq. Fl. Ind. Bat. Suppl. 439. 1861. Holotype, Sumatra, *Teysmann HB 716* (U); isotype (BO).

Ficus diepenhorstii (Miq.) King, Ann. Bot. Gard. Calcutta **1**: 181. 1888.

Prainea cuspidata Becc. For. Borneo 636. 1902. Holotype, Borneo, *Beccari PB 2825* (FI); isotypes (FI, K, P).

Prainea multinervia Merr. Philip. Jour. Sci. **29**: 364. 1926, Pl. Elmer. Born. 46. 1929. Holotype, Borneo, *Castro and Melegrito 1610* (UC, not seen); isotypes (A, BO, K).

Trees, height to 30 m. (60 m. fide *Gusdorf 115*), buttressed, bark dark red-brown, peeling off in flakes. *Twigs* 2–5 mm. thick, finely rugose, appressed puberulent, soon glabrescent. *Leaves* 10–33 × 4–13 cm., oblong, varying oblong- or obovate-elliptic, or elliptic, apex abruptly contracted or often subtruncate below a narrow acumen to 1.5 cm. long, base cuneate, or often oblique with one side subcordate, margin entire; midrib and lateral veins prominent beneath, intercostals slightly so, areolae often slightly bullate above; lateral veins 11–24 pairs, straight or slightly curved, inarching at margin conspicuous; intercostals forming rectangular net; glabrous, drying dark to pale reddish brown; petiole 8–22 mm. long.

Inflorescences solitary or paired in leaf-axils. *At anthesis*: *male head* c. 15 mm. across, globose; perianths tubular, perforate, 1.4 mm. long, minutely pubescent; stamen 1.8 mm. long, filament cylindric, anther oblong, 0.4 mm. long; bracts slenderly stalked, heads peltate, 0.3 mm. across, ciliate; peduncle 30–40 × 2 mm., glabrous to short-pubescent; *female head* with bifid styles exserted, branches 0.5 × 0.2 mm., forked at the tips. *Mature female head* to 35 mm. across (to 55 mm. including fruiting perianths), globose, loosely covered by numerous flowers and bracts, yellow-green, drying brown; fruiting perianths 8–20, projecting to

15 mm., ellipsoid, 10 mm. across, obtuse or broadly and obtusely attenuate; remaining perianths c. 4 mm. long, apices clavate, perforate, minutely pubescent, 1.5 mm. across; bracts slenderly stalked, heads spathulate, 0.3 mm. across, ciliate; peduncle 75–110 × 2–3 mm., puberulent.

VERNACULAR NAMES: *Tampang* (Malay), Sumatra, Borneo; *Limpato*, Sumatra.

DISTRIBUTION: in lowland evergreen forest to 1700 ft., Malaya, Sumatra, Borneo.

Malaya. KEDAH: Weng road, near Baling, *Best SFN 21266* (K, SING, infl.). **Sumatra.** ATJEH: Bivak Aer Putih, waterfall near Pendeng, Gajolanden, *Van Steenis 9270* (BO, L, ♀). WEST COAST: Fort Elout, *Teysmann HB 716* (BO, U); Priaman, *Diepenhorst HB 2092* (BO, L, U, ♀), *HB 2500* (BO, L, U, ♂), *HB 2914* (BO). INDRAGIRI: Batang Peranap, *bb 30095* (BO, L); Muara Serangge, *bb 30066* (BO, L); Peranap, *bb 30105* (A, BO, L). DJAMBI: Danau Lama, *bb 13639* (BO). PALEMBANG: Lematang Ilir, Gunong Megang, *NIFS T 340* (BO, L ♂), *NIFS T 521* (BO, K, L, U, ♀); Lematang Ilir, Semangus, *bb 32063* (A, BO, L, SING, ♂), *bb 32085* (A, BO, L, SING); Mulak Ulu, *Grashoff 323* (BO, L). LAMPONGS: Manggala, *Gusdorf 115* (BO, ♀). ENGGANO: forest near Bua bua, *Lutjeharms 4558* (A, BO, K, L, P, SING). **Borneo.** SARAWAK: Gunong Braam, near Sabungo, *Beccari PB 2825*, Nov. 1866 (FI, K, P, ♂, ♀). SOUTH AND SOUTHEAST BORNEO: Tanah Bumbu, Kampong Baru, *bb 13364* (BO). EAST AND NORTHEAST BORNEO: Berouw, Domaring, *bb 18817* (A, BO, L); Bulungan, Mara, *bb 10809* (BO); Upper Mahakam, D. Parei, *bb 20743* (A, BO, L). BRITISH NORTH BORNEO: Limanis, *Wood 1790* (BO, ♂); Tawao, Elphinstone Prov., *Elmer 21799* (A, BM, BO, GH, K, L, P, SING, U, ♀). BANGUEY ISLAND: *Castro & Melegrito 1610*, July–Sep. 1923 (BO, K, ♂).

The appearance of the mature female head is rather variable, owing to differences in the number of fruiting perianths and in the extent to which the other perianths elongate after anthesis. The leaf form in which the apex is subtruncate below the acumen is distinctive and is found only in this species of the genus.

4. **Prainea papuana** Becc. For. Borneo 635. 1902. Holotype, New Guinea, *Beccari PP 675* (FI); isotypes (FI).

Artocarpus papuanus Renner, Bot. Jahrb. **39**: 367. 1907, non Diels, 1936.

Prainea microcephala J. J. Smith, Bull. Jard. Bot. Buitenzorg III. **6**: 80. 1922. Syntypes, Ternate, *Beguin 691*, Halmaheira, *Beguin 1919*, *1980*, *2242* (BO); lectotype, *Beguin 1980* (BO).

Parartocarpus papuanus S. Moore, Jour. Bot. **61** Suppl. 52. 1923, non Becc. 1902; Diels, Bot. Jahrb. **67**: 175. 1936. Syntypes, New Guinea, *Forbes 331*, *411* (BM); lectotype, *Forbes 411* (BM).

Trees, height to 35 m., bark brown, peeling off in flakes. *Twigs* 2–3 mm. in diameter, finely rugose, appressed puberulent, soon glabrescent. *Leaves* 8–26 × 4–12 cm., oblong, varying elliptic, abruptly narrowed into an acumen to 1.5 cm. long, base cuneate or rounded, often oblique with one side subcordate, margin entire; midrib prominent beneath, lateral veins

slightly so, areolae often bullate on both surfaces; lateral veins 9–20 pairs, straight or slightly curved, inarching at margin conspicuous; intercostals not parallel; glabrous, drying red-brown, grey or green above, dark to pale brown beneath; petiole 8–18 mm. long.

Inflorescences solitary or paired in leaf-axils. *At anthesis*: *male head* 3–8 mm. across, globose; perianths tubular, clavate, shortly bilobed above, 1.8 mm. long, minutely pubescent; stamen 2.5 mm. long, filament slender, cylindric, anther oblong, 0.4 mm. long; bracts slenderly stalked, heads clavate, 0.4 mm. across; peduncle 15–60 × 2 mm., velutinous; *female head* olive green, with bifid styles exserted, branches 0.7 × 0.5 mm., obtuse. *Mature female head* 10–20 mm. across (excluding fruiting perianths), globose, loosely to compactly covered by c. 25–100 flowers and numerous bracts, orange, drying brown; fruiting perianths 2–12(–25), projecting to 10 mm., subglobose to conical, 10 mm. across, mucronate; remaining perianths c. 2.5 × 1 mm., clavate, mouth contracted, obtusely 4-lobed; bracts slenderly stalked, heads clavate, 0.5 mm. across, often coherent in groups; peduncle 30–90 × 2 mm., velutinous.

DISTRIBUTION: in lowland evergreen forest to 3500 ft., Moluccas (Halmaheira group), New Guinea.

Moluccas. MOROTAI: Gunong Moku, *Anang 263* (L); Mt. Permatang, along the Sangowo River, *Kostermans 959* (L, SING); Tjaw, *Kostermans 836, 837* (L). HALMAHEIRA: Galela, Soa Tobaru, *Beguin 1919*, Dec. 1921 (BO, K, L, U, ♀), *1926* (BO, L, ♀), *1980*, May 1922 (BO, L, P, SING, U, ♀); Kampong Toliwang, *Idjan/Moehtar 364* (K); W. Pitu, *Beguin 2242*, Nov. 1922 (BO, K, L, P, U). TERNATE: Laguna, *Beguin 691*, May 1920 (BO, L, ♀). BATJAN: Masurung, *bb 23133* (BO, L).

New Guinea. VOGELKOP: Andai, *Beccari PP 675*, 1872 (FI, ♂, ♀); Manokwari, Pomi, Kolonisatie, *bb 15897* (BO, ♀); n. of Ransiki, 80 km. s. of Manokwari, *Kostermans 4746* (A, K, L, SING, ♀); Sorong, *Beccari s.n.* (FI). DUTCH NORTH NEW GUINEA: Bernhard Camp, Idenburg River, *Brass & Versteegh 13167, 14122* (A, ♀). PAPUA. Central Division: Boridi, *Carr 14976* (SING, ♀); Koitaki, *Carr 12213* (BM, K, L, SING, infl.), *12586* (BM, K, SING, infl.), *12886* (BM, K, L, SING, ♀); Sogeri, *Forbes 331, 411*, 1885–6 (BM, K, L, ♀). Milne Bay District, Cape Vogel Peninsula: near Medino village on n. coast, *Hoogland 4666* (A, ♀); Menapi, *Brass 22000* (A, ♀). MANDATED TERRITORY OF NEW GUINEA. Morobe District: *Womersley NGF 2994* (A, BO K, L, ♀); Quembung, Sattelberg, *Clemens 8099* (A, ♀). D'ENTRECASTEAUX IS. Normanby I.: Lebudowa River, *Brass 25517* (K, L, ♀); Waikaiuna Bay, *Womersley & Brass NGF 8674* (A, K, ♀); near Waikaiuna Plantation, *Jackson NGF 4109* (A, K, L, SING, ♀). JAPEN: Serui, *bb 30434* (BO, L), *bb 30655* (L). LOUISIADE ARCHIP.: Misima I., Mt. Sisa, *Brass 27523* (K, L, ♀).

In his description of *Parartocarpus papuana*, S. Moore cited a third specimen, *Forbes 503*, but this has not been found either at the British Museum (Natural History) or elsewhere.

The female head in *Prainea papuana* shows a variability similar to that of *P. limpato* in the number of seeds formed and in the degree of elongation of the perianths after anthesis. The latter is partially correlated with

a geographical variation in the diameter of the head at anthesis. In eastern New Guinea the female head then has a diameter of 10–15 mm. and the surface generally remains compact at maturity, but in the Vogelkop and the Moluccas the diameter is only about 5 mm. at anthesis and later all the flowers usually elongate somewhat so that at maturity the surface becomes loose. A parallel variation occurs in the size of the male head. However, the collections from Dutch North New Guinea are intermediate, with a diameter of 8–10 mm. at anthesis and with the surface remaining fairly compact. The creation of subspecies is therefore not regarded as justifiable.

SPECIES EXCLUDENDA

Prainea rumphiana Becc. For. Borneo 636. 1902 = **Artocarpus fretissii** Teysm. & Binnend. Abh. Naturf. Ges. Halle 9: 189. 1866.

A DISCUSSION OF THE PACIFIC RAILROAD REPORTS AS ISSUED IN THE QUARTO EDITION

SUSAN DELANO MCKELVEY

THE VOLUMES CONSIDERED in these pages contain the findings of those who participated, both in field and in laboratory, in the first systematic examination by the United States government of the immense area extending from the Mississippi River to the Pacific Ocean and from Canada on the north to Mexico on the south, and which, in the half century from 1803 to 1853 had become part of our national domain.

The only official expeditions yet to have crossed the region, those of Lewis and Clark and of Frémont, had acquired, everything considered, some interesting scientific facts, but these were inadequate when it became necessary to determine "the most practicable and economical route" for a railroad.

For the factor of practicability, concerned with such matters as grades, distances, and weather conditions, demanded trained topographers, astronomers and meteorologists; while the factor of economy, interlocked to be sure with the practicable, but even more intimately related to a railroad's construction and maintenance as well as to the subsistence of prospective settlers along its line of march, necessitated knowledge, in terms of identification, of rocks, minerals, soils, timber, plants and all forms of animal, bird, fish and reptilian life, as well as estimates of their abundance and availability. Such facts could only be supplied by geologists, mineralogists, botanists, zoologists and others proficient in the natural sciences, at that time a covering term for all that related to the systematic study of nature as a whole, whether animal, vegetable or mineral.

On earlier official expeditions the government had demonstrated little enthusiasm when asked to include men interested in such matters. Now the expert knowledge which only they could supply had become vital and the Smithsonian Institution and its members were called upon to provide instructions in the technicalities of field collecting — the making of the specimens and the keeping of the records upon which the reports of the scientists must of necessity be based — and to enumerate the equipment necessary for its accomplishment. This they did, wholeheartedly, even specifying red pencils and stressing the importance of adding tartar emetic to all alcohol — "besides adding to its preservative powers, [this] will remove any temptation to drinking it on the part of unscrupulous persons."

Because the expeditions were to cross the trans-Mississippi West at, or near, four widely separated parallels of north latitude, a comprehensive coverage was assured as far as natural history collections were concerned and the scientific reports, some including fine plates, which eventually were appended to those descriptive of the routes and which were written by such authorities as S. F. Baird, W. P. Blake, J. S. Newberry, J. Torrey,

Asa Gray and many others, constituted and still must be regarded as invaluable records.

Although publications dealing with special aspects of the surveys never fail to mention that important scientific work was accomplished, they do not elaborate upon the statement. Long interested in collectors — often ignored to the point of anonymity — I determined, with the optimism of ignorance, to "run through" the series of reports, twelve volumes in thirteen, and see what could be learned of the men upon whose accomplishments in the field the scientific edifice was erected. The great quarto edition, occupying three to four feet of standing room, has been characterized as "monumental," "sumptuous" — it has been stated [1] that its publication cost the government over one million dollars, the surveys themselves four hundred and forty-five thousand — and, although its pristine magnificence is no longer in evidence, its very dimensions may have contributed to my confidence that the content would be well organized, clearly presented and easily digested. This did not prove to be the case and any "running through" was reduced to a walk and eventually a full stop, for, with a mental preference to understand one thing before proceeding to another, I was soon "bogged down" in the fine points of military terms and distinctions, as well as in far deeper swamps.

It finally became clear that, before attempting any study of the reports, three preliminary tasks must be faced: first, the government documents in which they were issued must be understood; second, the content of all volumes of the series must be analysed in order to be able to cite accurately from their pages; and, third, a satisfactory means of locating the data contained in the analyses must be devised. These tasks were completed for my own enlightenment and convenience. But, convinced that anyone approaching the reports for the first time must be faced with similar needs to mine, it is possible that my findings may have a wider usefulness. I shall comment upon what these three tasks involved before turning to their solution which constitutes my paper proper.

(1) The issues of the quarto edition have been enumerated before now. But because enumerations vary greatly in form of presentation, it was necessary to compare and to check, one against the other, a number of authoritative bibliographies in order to feel certain that an accurate and complete picture had been obtained — a slower task than the brevity of my summary might indicate.

Especially helpful to this end were the presentations contained in Mr. George Leslie Albright's "Official explorations for Pacific railroads 1853–1855," issued in 1921 (*University of California Publications in History*, Volume X), in a *Catalog of books represented by Library of Congress printed cards*, published in 1948 (Ann Arbor, Michigan, Volume 154, 634–635), and in Professor Howard Taft's *Artists and illustrators of the Old West 1850–1900*, published in 1953 (Charles Scribner's Sons, New York). Another volume, the *Checklist of United States public documents* (edition

[1] *See* Taft, H., *op. cit.* this page, (5 & *fn.* 13).

3. 1: 1274–1275), published in 1911, which distinguishes all numbered Congressional Documents by Serial Set and Serial Number, served as a final check. These authorities are occasionally referred to in my paper.

(2) Examining the quarto edition for the first time, problems inherent in its makeup became apparent immediately. I mention some of the more baffling:

There is no index covering the content of the entire series, and understandably so. For, with the exceptions of Volumes VIII, IX and XI, none has pages numbered consecutively throughout — Volumes II and X, for examples, have seven sets of page numbers each — and it is therefore necessary, and I believe always will be necessary, to "leaf through" a volume to locate an included report. Although page numbers in individual reports are for the most part clear, seemingly endless blank or only occasionally numbered pages, in front or back matter especially, are, at best, an annoyance if one needs to cite therefrom.

Because it had been impossible, obviously, to assemble on time for a waiting printer, the great amount of material due from widely scattered sources, reports are not always present where a volume's table of contents indicates and subsidiary papers, usually scientific, are not always found in proximity to the report to which their content relates. A note on an inserted page or an easily overlooked footnote states that such and such a paper will appear later, although when or where is not predicted. Only by time-consuming search through later volumes — involving in all instances the "leafing through" procedure already mentioned — can matter delayed in publication be located; it should be added that, when found, it is usually referred to its appropriate place in an earlier volume!

And what is true of belatedly published papers is also true of matter elucidating the content of reports, whether this be in the form of plates of all sorts, of maps, of profiles, etc. Such material is usually enumerated in a report's list of illustrations, but checking often proves that certain items are lacking, or missing at the point indicated. To enumerate the discrepancies in illustration-content existing in the many issues of any one volume — they appear to have been dictated by the convenience, or perhaps necessity of a volume's compiler — was clearly impossible. One could not hope to do more than supply the total number included in the report under scrutiny and, when such existed, their numerical captions.

Attempts to record the whereabouts of a report's scattered but affiliated content, textual and illustrative, resulted in the analyses contained in this paper. That they were essential became evident when cross-references necessitated accurate citation. Furthermore, although analyses could not do away with the broken pagination of the volumes, an irremediable problem, they could lessen some of the other difficulties inherent in the makeup of the series; for to be able to ascertain, within the compass of a few pages, the content of its volumes, would certainly be far more convenient than to search repeatedly through the ponderous tomes themselves.

Two other matters related to the compilation of the volumes had best

be mentioned here — others will be referred to at appropriate places in my analyses.

The first concerns dates of publication. The printers were obliged to proceed with their tasks; consequently the year supplied on the main title page of a given volume may be earlier than one recorded on an included letter, report, etc. When, in my analyses, later years than those which appear on the title pages are recorded, they are based on this internal evidence and merely represent the year before which, it may be assumed, a given volume could not have been issued. For one example see under Volume II.

To scientists dates of publication can be immensely important. Dr. I. M. Johnston's paper, "Publication dates for botanical parts of the Pacific Railroad Reports" (*Journal of the Arnold Arboretum*, Volume XXIV, 237–242, 1943), assigns, on the strength of records found in old letters, contemporary publications and the like, "Reasonably exact dates to the various botanical reports, accurate in most cases to within a month or two." Dr. Johnston also takes into consideration the first, or octavo edition of the reports, an issue not discussed in this paper. (*See* my *fn.* 3.) His conclusions are summarized in tabulated form at the end of his paper.

Only in rare instances do the authors of scientific reports included in the quarto series mention the publication date of their papers. When they do so the fact is noted in my analyses.

The second matter relates to the manner in which certain illustrations are incorporated in the volumes. Because of the great number contained in Volume XI the unfortunate results are especially apparent and my comments are confined to that volume, although to a lesser degree the criticism is applicable wherever similar illustrations are included.

Volume XI is, in text, perhaps the most generally useful in the entire series of *Pacific Railroad Reports*. It is regrettable, therefore, that its associated and very fine maps, profiles, panoramic views, etc., representing the graphic results of the topographers' arduous task, should have been included in a manner which makes their manipulation impossible and is destructive of the illustrations themselves. Most are extremely large and many-times-folded. Bound tightly in with and outbalancing the text which constitutes the first half of the volume, to unfold them, to keep any single one spread out for study or any two for comparison, and to execute the even more difficult refolding without tearing, are all impossibilities. Yet, because none bears any exterior notation, they must be opened to full size for identification — the placement of the beautifully lettered and explicit captions seems to have been selected to that very end! Even in copies of Volume XI which have obviously stood unused, many of the illustrations have already disintegrated along their exposed, uneven folds; lack of dusting or the reverse may have been responsible, or possibly the paper was not suitable in the first place. Had they been mounted on linen (*see fn.* 4), visibly captioned to conform to the enumeration found in the volume's "Contents," and supplied loose in a container, their usefulness would have been assured and their life expectancy prolonged; as issued,

they symbolize endless labor and much money spent to little purpose. It is possible that in some instances these valuable records might still be mounted although in others it could not be done now.

(3) The Ann Arbor *Catalog*, cited on p. 39, supplies two synopses which serve as guides to the content of the quarto edition. The first, "Contents (Outline)," condenses into some 15 lines the routes described in its volumes, usually according to the parallels which they followed. The second, "Contents (By authors)," supplies an alphabetical list of the men who contributed reports, and then records, for the most part by a descriptive term, the subject matter of their papers, followed by the volume or volumes in which they are to be found. Presumably intended to supplement each other, these synopses presuppose a very great familiarity with the content of the series and, in my opinion, are not sufficiently explicit to offer much assistance to anyone approaching the reports for the first time. Moreover, necessitating frequent reference to the volumes themselves, they present many of the already mentioned difficulties inherent in the edition's makeup.

The "Alphabetical index of authors" which concludes this paper supplies, I believe, a more complete roster of contributors than does the somewhat similar list of the *Catalog*. And, when used in conjunction with my analyses, it provides, without reference to the volumes themselves, the precise association of every report as well as an outline of that report's entire subject matter and the pagination thereof. In possession of these facts one should be sufficiently informed to be able to turn immediately to the appropriate volume as well as to the information sought in any given report.

REPORTS OF EXPLORATIONS AND SURVEYS TO ASCERTAIN THE MOST PRACTICABLE AND ECONOMICAL ROUTE FOR A RAILROAD FROM THE MISSISSIPPI RIVER TO THE PACIFIC OCEAN [2]

An enumeration of the Congressional Documents containing the reports. An analysis of the content of the twelve volumes, in thirteen, of the quarto edition in which the reports were issued in final form. An alphabetical index of authors to be used in conjunction with the analyses.

CONGRESSIONAL DOCUMENTS CONTAINING THE REPORTS

Although a few of the *Pacific Railroad Reports* enumerated below were issued in an octavo edition,[3] the revised, complete and authoritative

[2] Present on the title-page of every volume in the series as well as on the title-pages of included reports, this is inconveniently long for repeated citation and is usually shortened to *Pacific Railroad Reports*, an abbreviation which G. K. Warren used as early as 1859 in his table of contents of Volume XI, [5].

[3] The *Checklist of United States public documents* states, "Some of the . . . reports first appeared in 8° in House Document 129, 33d Congress, 1st session, in serial nos. 736, 737, and 739. Serial no. 738, the projected v. 3 of this edition, was never printed." *See* p. 39.

reports, the ones usually cited and the ones most often found in libraries, were prepared under the direction of the War Department and were issued for both Senate and House of Representatives in a quarto edition of twelve volumes, in thirteen, under the long descriptive title cited above.

The quarto edition is found as follows:

Volumes I through XI: *33d Cong., 2d Sess., Senate Ex. Doc. No. 78* [Serial Nos. 758 through 768[4]]; *33d Cong., 2d Sess., House Ex. Doc. No. 91* [Serial Nos. 791 through 801].

Volume XII: *35th Cong., 3d Sess., Senate Ex. Doc. No. 46* [Serial No. 992[5]]; *36th Cong., 1st Sess., House Ex. Doc. No. 56* [Serial Nos. 1054, 1055[6]].

All the issues cited above are numbered Executive Documents and are included in the Serial Sets.

There are, in addition, two printings, one of Volume XI, one of Volume XII, which lack document numbers and are not included in the Serial Sets. These are:

Volume XI: *36th Cong., 2d Sess., Senate Ex. Doc.*[7]
Volume XII: *36th Cong., 1st Sess., Senate Ex. Doc.*[8]

There may be variations in these unnumbered issues, related primarily to such matters as the date of publication on a volume's title-page, their illustration-content or illustration-placement and so on, but as far as text is concerned, all issues, whether numbered or unnumbered documents, appear to be accepted as the same.

AN ANALYSIS OF THE CONTENT OF THE THIRTEEN VOLUMES OF THE QUARTO EDITION

Volume I — 1855

33d Cong., 2d Sess., Senate Ex. Doc. No. 78 [Serial No. 758[9]]

The title-page of *Pacific Railroad Reports*, Volume I, is dated 1855. No included matter bears a later date.

Some parts, certainly, of the reports must have been issued for the Senate in this octavo, unillustrated, and preliminary edition; for example: *33d Cong., 1st Sess., Senate Ex. Doc. No. 52* [Serial No. 698]. *See* Albright (45, *fn.* 1; 160), and Taft (255, *fn.* 13).

[4] Taft (255, *fn.* 2) records: ". . . The maps in the Senate Serial Set (768[1] and 768[2]) of volume 11 are mounted on linen . . . requiring two books (parts 1 and 2) to contain them." It has not been possible to locate a copy of Volume XI with mounted maps in the libraries of Boston or of Cambridge and the issue must be rare.

[5] Taft (255, *fn.* 4) states: "This volume (Serial No. 992) duplicated in a single book the material in Serial Nos. 1054, 1055 [see below] but is designated on the title page as 'Supplement to Volume 1' ". Card 2 of the Ann Arbor *Catalog* notes that this "Supplement to vol. I," was issued in 1859, W. A. Harris, printer.

[6] The two volumes of this issue are distinguished on the respective title-pages of *Pacific Railroad Reports* as Volume XII. Book I, Volume XII. Book II.

[7] The title-page records that this was printed in Washington by George W. Bowman and is dated 1861. The maps are bound in with the text. *See* Taft (255, *fn.* 2).

[8] The title-page records that this was printed in Washington by Thomas H. Ford and is dated 1860. As in *House Ex. Doc. No. 56* its two parts (Book I and Book II) are bound separately, making two volumes. *See* Taft (255, *fn.* 3).

[9] Because my analyses have been based upon a mixed set of the quarto edition, the

"Contents of Volume I," [iii], lists five papers. The subject matter of the first four, distinguished here as (1) through (4), is enumerated in the "Index to Report of the Secretary of War and Office Reports," [v]–viii, and that of the fifth, (5) below, in the "Alphabetical Index to Governor Stevens's Report," [637]–651. Page numbers run consecutively in (1) through (4); in (5) they are independently numbered.

The title-pages of (1) through (5) read respectively:

(1) Report of the Secretary of War on the several railroad explorations. [1]–35.

For reprintings of portions of this report *see* "Explanatory note" quoted under Volume III, *fn.* 18.

(2) An examination by direction of the Hon. Jefferson Davis, Secretary of War, of the reports of explorations for railroad routes from the Mississippi to the Pacific, made under the orders of the War Department in 1853–'54, and of the explorations made previous to that time, which have a bearing upon the subject: by Capt. A. A. Humphreys & Lieut. G. K. Warren, Corps of Topographical Engineers. [35]–111.

CONTENTS: Table of contents, [35]; An examination of the reports of explorations for railroad routes from the Mississippi to the Pacific, [37]–38; Humphreys & Warren report (6 chapters), [39]–111.

For reprintings of portions of this report *see* "Explanatory note" quoted under Volume III, *fn.* 18.

(3) Memoranda on railways, prepared Office of Pacific Railroad Surveys; by Capt. Geo. B. McClellan, Corps of Engineers, under instructions from Hon. Jefferson Davis, Secretary of War. [113]–130.

(4) Report upon the cost of transporting troops and supplies to California, Oregon, New Mexico, etc., etc. By Major General Thomas S. Jesup, Quartermaster General, U.S. Army. [131]–134.

(5) Report of explorations for a route for the Pacific railroad, near the forty-seventh and forty-ninth parallels of north latitude, from St. Paul to Puget Sound. By I. I. Stevens, Governor of Washington Territory. [i]–vii; [1]–651.

CONTENTS: Table of contents, [iii]–vii; Part I. Reports from the field, [1]–72; Part II. Report (18 chapters), [73]–159; Miscellaneous documents related to special aspects of the survey,[10] 160–635; Note, [636]; Alphabetical index to Governor Stevens's report. Prepared by E. B. Hunt, U.S.A., [637]–651.

For maps and profiles *see* under Volume XI.

A "Note," [636], states: "The Narrative of the Explorations, accompanied by Views, illustrating the Features of the country, the Natural History, Botanical and other Scientific Reports, with Illustrations, will be found in a Subsequent Volume." *See* under Volume XII, Books I and II.

one in the Arnold Arboretum Library, the printing is cited in every instance to facilitate checking should such be desired.

[10] For authors of certain of these documents *see fn.* 56.

Volume II — 1857

33d Cong., 2d Sess., House Ex. Doc. No. 91 [Serial No. 792]

The title-page of *Pacific Railroad Reports*, Volume II, is dated 1855, but Pope's "Explanatory note" to Blake's geological report, inserted before the title-page of (4A) below, is dated February 18, 1857.

"Contents of Volume II," [iii], lists six papers, distinguished here as (1) through (6); a seventh, (4A) below, is not listed. Each of these seven papers has its own set of page numbers. They are cited on their respective title-pages as follows:

(1) Report of explorations for a route for the Pacific railroad, by Capt. J. W. Gunnison, Topographical Engineers, near the 38th and 39th parallels of north latitude, from the mouth of the Kansas River, Mo., to the Sevier Lake, in the Great Basin. Report by Lieut. E. G. Beckwith, Third Artillery. [1]–128. 13 Plates (captioned but not numbered).

CONTENTS: Introductory letter, [3]; Contents, [5]–8; Report (10 chapters), [9]–118; Appendix A. Letters relating to the progress of the survey of the route near the 38th and 39th parallels, in charge of Captain Gunnison, [119]–124; Appendix B. Explanations of the map and illustrations, [125]–128.

For associated botanical report *see* under (2) below. For associated zoological reports *see* under Volume X. For maps and profiles *see* under Volume XI.

(2) Report of explorations for a route for the Pacific railroad, on the line of the forty-first parallel of north latitude. By Lieut. E. G. Beckwith, Third Artillery. [1]–132.

CONTENTS: Introductory letter, [3]; Contents,[11] [5]–8; Report (10 chapters),[12] [9]–112; Appendix. Instructions from the Secretary of War, [113]–114; Botanical report, [115]–132.

For zoological reports *see* under Volume X. For plates, maps, profiles, *see* under Volume XI.

The title-page of the included Botanical report reads:

Report on the botany of the expedition: by John Torrey and Asa Gray. [115]–132. 10 plates (Nos. I–X).[13]

CONTENTS: Contents, [117]; Botanical report, Part I, [119]–125; Part II,[14] 125–131; Explanation of the plates, 131–132.

(3) Synopsis of a report of the reconnaissance of a railroad route from

[11] For "Errata" see p. 8, and for "Additional errata" *see* sheet inserted between pp. 8 and [9].

[12] Of these Chapter X, "Geology," includes 4 plates of fossils (Nos. 1–4) and 3 woodcuts.

[13] Of these, No. I is associated with (2), Nos. II–X with (1).

[14] Part I describes collections made under (2) and Part II collections made under (1). For the wording of the long descriptive headings of Parts I and II, *see Pacific Railroad Reports*, Volume II, where the heading of Part I appears on pp. 117, 119, and that of Part II on pp. 117, 119, 125.

Puget Sound via South Pass to the Mississippi River: by Fred W. Lander, Civil Engineer. [1]–45.

CONTENTS: Contents, [3]; Legislative and executive action in reference to this exploration and report, [5]–6; Introduction, [7]–28; Report, [29]–45.

(4) Report of explorations of a route for the Pacific railroad, near the thirty-second parallel of north latitude, from the Red River to the Rio Grande, by Brevet Captain John Pope, Corps of Topographical Engineers. [i]–iv; [1]–185.

CONTENTS: Pope letter transmitting report, [ii]; Contents, [iii]–iv; Report (8 chapters), [1]–50; 12 Appendices (A through L),[15] [51]–156; Botanical report, [157]–178; Index, [179]–185.

For map and profile *see* under Volume XI.

The title-page of the included Botanical report reads:

Report on the botany of the expedition: by John Torrey and Asa Gray. [157]–178. Index,[16] [179]–185.

Associated with the route described in (4) but with its own set of page numbers is:

(4A) Report on the geology of the route, near the thirty-second parallel: prepared from the collection and notes of Capt. Pope, by William P. Blake, Geologist of the Office of the United States Pacific Railroad Surveys. [1]–50. Geological map. Geological section.

CONTENTS: Explanatory note to geological report[17] [inserted before title-page]; Blake letter submitting his report, [3]; Contents, [5]–6; Report (6 chapters), [7]–40; Catalogue of the geological collection made by Brevet Captain John Pope, 1853, [41]–42; Note in explanation of the map and section, [43]–44; Index to the report on the geology of the route near the thirty-second parallel, [45]–50.

(5) Report of explorations for that portion of railroad route, near the thirty-second parallel of north latitude, lying between Dona Ana, on

[15] Most of these are highly technical. Four, however, have a general interest: "Appendix A. Diary of the expedition, by J. H. Byrne, Assistant Computer," [51]–95, and "Appendix E. Table of camping places along the direct line of survey," [98]–99, are both helpful guides to Pope's route.

"Appendix B. Preliminary report on the natural history," [94], signed by Spencer F. Baird, refers to the scope and importance of Pope's zoological collection, and to anticipated publications thereon.

"Appendix D. Note upon the geological report," [98], concerns the delayed publication of Blake's report upon the geological collection, and the preliminary report of Jules Marcou in the octavo edition of *Pacific Railroad Reports*. *See* under (4A) below.

[16] This covers matter contained in Pope's report proper as well as in the botanical report.

[17] Pope wrote: "The mineralogical collections made by me were placed in the hands of M. Jules Marcou for examination, and carried by him to France. They were subsequently returned in a confused condition, and with many of the labels displaced. This fact will account for many errors in the report, map, and section prepared by Mr. Blake." This is dated Washington, February 18, 1857.

the Rio Grande, and Pimas Villages, on the Gila. By Lieut. John G. Parke, Corps of Topographical Engineers. [1]–28.

CONTENTS: Report, [3]–24; Appendix (in two parts, A and B), [25]–26; Index, [27]–28.

For Parke's later report *see* under Volume VII.

(6) Extract from report of a military reconnaissance, made in 1846 and 1847, by Lieut. Col. W. H. Emory. [1]–22.

CONTENTS: Humphreys letter explaining the inclusion of this earlier report, [3]; Extract from Lt. Col. Emory's report, [5]–20; Index, [21]–22.

Volume III — 1856

33d Cong., 2d Sess., House Ex. Doc. No. 91 [Serial No. 793]

The title-page of *Pacific Railroad Reports*, Volume III, is dated 1856. No included matter bears a later date.

Volume III has five sets of page numbers.

"Contents of Volume III," [1], divides the subject matter into two parts, distinguished here as (1) and (2). The first bears the heading:

(1) Extracts from the (preliminary) report of explorations for a railway route, near the thirty-fifth parallel of north latitude, from the Mississippi River to the Pacific Ocean, by Lieutenant A. W. Whipple, Corps of Topographical Engineers. [3]–36.

CONTENTS: Explanatory note,[18] [3]; Extracts, [3]–32; [Portion of] Appendix B. Table containing the distances, altitudes, * * * * of each camp from Fort Smith to the Pacific Ocean, 33–36.

The title-page of the second reads:

(2) Report of explorations for a railway route, near the thirty-fifth parallel of north latitude, from the Mississippi River to the Pacific Ocean: by Lieutenant A. W. Whipple, Corps of Topographical Engineers; assisted by Lieutenant J. C. Ives, Corps of Topographical Engineers.

CONTENTS: [19] Letter to the Secretary of War, [vii]–viii; General

[18] Signed by Humphreys, the "Explanatory note" reads: "The reports of the Secretary of War and the revising officer, which appear in volume one, were founded, so far as they relate to the route near the 35th parallel, upon the preliminary report of Lieutenant Whipple. The following chapters, being those which are principally referred to in those revisory reports, are, therefore, republished. They are chapters two, three, four, five, and eleven, with a portion of appendix B. The preliminary profiles are also reprinted."

For "preliminary report of Lieutenant Whipple," *see* octavo edition of *Pacific Railroad Reports* (*House Ex. Doc. No. 129*). For "reports of the Secretary of War and the revising officer which appear in volume one" *see* under that volume. Reprintings of the "preliminary profiles" have not been located in the printings of the quarto series examined.

[19] Page numbers in front matter preceding Part I appear to be confused but are cited as given.

table of contents,[20] [ix]–x; Part I, [i]–viii; [1]–136; Part II, [1]–77; Part III, [1]–127; Part IV, [iii]–xiii, [1]–175.

The title-pages of Parts I, II, III and IV read respectively:

Part I. Itinerary. [i]–viii, [1]–136. 10 plates (captioned but not numbered). 10 woodcuts.

CONTENTS: Errata, [iv]; Contents, [v]–vii; Illustrations, [viii]; Introduction, [1]–4; Itinerary (16 chapters), [5]–136.

Part II. Report of the topographical features and character of the country. [3]–77. 2 plates (captioned but not numbered). 2 woodcuts. 8 plates (diagrams, Nos. 1–8).

CONTENTS: Contents, [5]; Illustrations, [6]; General sketch of the route, [7]; Sections I through VII (of the route), [8]–45; General remarks upon various subjects, [45]–77.

For Maps and profiles *see* under Volume XI.

Part III. Report upon the Indian tribes, by Lieut. A. W. Whipple, Thomas Ewbank, Esq., and Prof. Wm. W. Turner, [1]–127. 7 plates (captioned but not numbered). 30 woodcuts. 3 maps (Nos. 1, 2, 3; inserted in text).

CONTENTS: Contents, [3]; Illustrations, [5]; Report (7 chapters), [7]–127.

Part IV. Report on the geology of the route, [i]–[xiii]; [1]–175. 3 plates (1 in text, unnumbered; for Nos. I, II, fossils, *see fn.* 21); 18 woodcuts. Geological map. 2 Geological sections. 9 small Geological sections (included in No. 2 below).

CONTENTS: Contents, [v]–vii; Illustrations, [viii]; Errata and addenda, [ix]; Additional errata, [xi]; Introductory letter (to No. 1), [xiii]; No. 1. General report upon the geological collections. By William P. Blake, Geologist of the Office of the United States Pacific Railroad Explorations and Surveys (10 chapters),[21] [xiii]; [1]–116; Catalogue of the geological collection, [117]–119; No. 2. Resumé and field notes, by Jules Marcou,[22] Geologist and Mining Engineer to the expedition; with a translation by William P. Blake, [121]–164; Resumé of a geological reconnaissance, extending from Napoleon, at the junction of the Arkansas with the Mississippi, to the Pueblo de los Angeles, in California. By Jules Marcou, Geologist and Mining Engineer,[23] [165]–175.

[20] This covers the subject matter of the entire Whipple report, Parts I through VI and its 13 Appendices (A through I, K through N), but only Parts I through IV are included in Volume III. For Parts V, VI and Appendices *see* under Volume IV.

[21] Chapter IX, [99]–105, is headed: "Descriptions and notices of the fossils collected upon the route. By Professor James Hall." It contains 2 plates (Nos. I, II).

[22] A "Note," [121], reads: "This paper is a copy of Mr. Marcou's field-book, and is an exact transcript of the original rough notes as they were taken while on the road or in camp."

[23] *Fn.* 1, [165], states: "This resumé is reprinted from the preliminary or first report of Lieutenant Whipple, in 8vo., Chap. VI, p. 40. (Reports of Pacific Railroad Surveys, House Doc. 129: Washington. 1855.)"

Volume IV — 1857

33d Cong., 2d Sess., House Ex. Doc. No. 91 [Serial No. 794]

The title-page of *Pacific Railroad Reports*, Volume IV, is dated 1856, but the "Introduction" to Part V, No. 4, [59], is dated January 12, 1857.[24]

Volume IV has three sets of page numbers.

It is a continuation of the Whipple report begun in Volume III and includes Part V, Part VI, No. 1, and "Appendices to report." These subdivisions are distinguished here as (1), (2) and (3) and their title-pages read:

(1) Part V. Report on the botany of the expedition. [i]–vii; [1]–195.

CONTENTS: Contents, [v]–vii; Nos. 1, 2, 3, 4, [1]–167; Index to botany, [169]–182; No. 5, [185]–193.

For included botanical profile and for plates *see* under Nos. 2, 3, 4, 5, below.

Part V includes five papers, headed respectively:

No. 1. General description of the botanical character of the country. By J. M. Bigelow, M.D. [1]–16.

No. 2. Description of forest trees. By J. M. Bigelow, M.D. [17]–26. Botanical profiles.

No. 3. Description of the Cactaceæ. By George Engelmann, M.D., of St. Louis, and John M. Bigelow, M.D. [27]–58. 24 plates (Nos. I–XXIV).

CONTENTS: No. 3, [27]–53; Explanation of the plates of Cactaceæ, [54]–58.

No. 4. Description of the general botanical collections. By John Torrey. [59]–182. 25 plates (Nos. I–XXV).

CONTENTS: Introduction, [59]; No. 4, [61]–161; Explanation of the plates, [163]–167; Index to botany, [169]–182.

No. 5. Description of the mosses and liverworts. By W. S. Sullivant. [185]–193. 10 plates (Nos. I–X).

CONTENTS: No. 5, [185]–191; Explanation of the plates, 192–193.

(2) Part VI. Report on the zoology of the expedition. [1]–17.

This includes one paper, headed:

No. 1. Field notes and explanations. By C. B. R. Kennerley, M.D., Physican and Naturalist to the expedition. [5]–17.

An inserted sheet, following p. 17, bears a "Note," reading: "*The remainder of the Zoological Report will appear in a subsequent volume, it being impossible to prepare it in time for publication in connexion with the other portions of this report.*"

For Part VI, Nos. 2, 3, 4, 5, *see* under Volume X.

[24] *See* under Whipple report, *Part VI. Zoological report* (Volume X, [7], *fn.*), where it is stated — it would seem incorrectly — that No. 1 ". . . appeared in Vol. IV, 1856."

(3) Appendices to report. [1]–288.

These 13 appendices are distinguished by the letters A through I, K through N, and consist, according to a "Note" [3], of ". . . the original unreduced records of the astronomical, magnetic, and meteorological observations. . ."

Volume V — 1857

33d Cong., 2d Sess., Senate Ex. Doc. No. 78 [Serial No. 762]

The title-page of *Pacific Railroad Reports*, Volume V, is dated 1856, but the title-page of Part II. Geological report, is dated 1857 and Blake's letter transmitting that report is dated April 6, 1857.

Volume V has four sets of page numbers.

The title-page, covering the content of Volume V, reads:

Report of explorations in California for railroad routes, to connect with the routes near the 35th and 32d parallels of north latitude, by Lieutenant R. S. Williamson, Corps of Topographical Engineers.

Front matter preceding and following this title-page and related to Williamson's report in its entirety appears on 12 unnumbered pages and includes the following: Contents of Volume V; Letter to the Secretary of War; General table of contents; Introduction. Instructions from the War Department.

The "General table of contents" divides the report into Parts I, II, III and IV, and three Appendices (A, B, C). These subdivisions, distinguished here as (1), (2), (3), (4) and (5), are cited on their respective title-pages as follows:

(1) Part I. Report. [1]–43. 12 plates (Nos. I–XII). 12 wood engravings.

CONTENTS: Contents, [5]; Illustrations, [5]; Report, [7]–43.

For maps and profiles *see* under Volume XI.

(2) Part II. Geological report, by William P. Blake, Geologist and Mineralogist to the expedition. [i]–xvi; [1]–370; [i]–xiii.

CONTENTS: Blake letter submitting the report, [v]; Contents, [vii]–xii; [Contents of] Appendix, [xiii]; Illustrations, xiv–xvi; I. Itinerary, [1]–130; II. Geology of portions of the route, [131]–310; Appendix (Articles I through VII), [311]–370; Index, [i]–xiii.

For maps, sections, plates, wood engravings, *see* under I. Itinerary; II. Geology of portions of the route; and Appendix (Articles I, II, III, V and VII).

The three subdivisions of the Geological report are cited on their respective title-pages as follows:

I. Itinerary, or notes and general observations upon the geology, mineralogy, and agricultural capabilities of the route (10 chapters, I–X), [1]–130. 9 plates (Nos. I–IX). 53 wood engravings.

II. Geology of portions of the route (10 chapters, XI–XX). [131]–310. 8 plates (3 maps, 4 views, section). 34 wood engravings. Geological sections. Geological map.

Appendix. [311]–370.

For plates *see* under Articles I, II, III, V, VII, below.

The Appendix includes seven Articles (of a contemplated eight) which are headed respectively:

Article I. Notice of fossil fishes. By Professor Louis Agassiz. [313]–316. 1 plate (No. 1).

Article II. Description of the fossil shells.[25] By T. A. Conrad. [317]–329. 8 plates (Nos. II–IX).

Article III. Catalogue of the recent shells, with descriptions of the new species. By Augustus A. Gould, M.D. [330]–336. 1 plate (No. XI).

Article IV. Letter from Professor J. W. Bailey, describing the structure of the fossil plant from Posuncula River. [337].

For plate (No. XII, figs. 1, 2) *see* under Article V.

Article V. Description of the fossil wood from the Colorado Desert. By Prof. Geo. E. Schaeffer. [338]–339. 1 plate (No. XII, figs. 1–4).

Article VI. Chemical examination of soils and incrustations. By J. D. Easter, Ph.D. [340]–358.

CONTENTS: Article VI, 340–343; Catalogue of the geological collection with descriptions of several of the specimens, [343]–358.

Article VII. Description of plants collected along the route, by W. P. Blake, and at the mouth of the Gila.[26] By John Torrey. [359]–370. 10 plates (Nos. I–X).

CONTENTS: Article VII, [359]–367; Description of the plates, [368]–370.

Article VIII.[27]

(3) Part III. Botanical report: by E. Durand and T. G. Hilgard, M.D. [1]–15. 18 plates (Nos. I–XVIII).

(4) Part IV. Zoological report.[28]

[25] A *fn.* states: "These descriptions were published in 1855. See Appendix to the Preliminary Geological Report, 8vo; Washington, 1855."

[26] An introductory paragraph, [359], signed by Torrey, mentions that the collection included, in addition to those of Blake, plants ". . . collected near Fort Yuma, by Major Thomas and Lieutenant Du Barry, of the United States army . . ."

[27] A page inserted at this point bears a "Note" reading: "Article VIII was not received in time for publication with the other portion of this report."

Article VIII has been cited in the contents of the Appendix (Part II. Geological report, [xiii]), as: "Description of fossil microscopic organism, from Monterey: By Professor J. W. Bailey." It has not been found in the series of *Pacific Railroad Reports* examined.

[28] A "*Note*" following the above title-page states: "The Zoological Report will appear in a subsequent volume, it being found impossible to prepare it in time for publication in connexion with the other parts of this report."

According to the "General table of contents" of Volume V, Part IV should have included the following papers: "No. 1. Mammals, by Professor S. F. Baird"; "No. 2. Birds, by Dr. A. L. Heermann, Physician and Naturalist to the expedition"; "No 3.

(5) Appendices. [1]–14.

CONTENTS: Appendix A. Distances and altitudes, [3]–4; Appendix B. Latitudes and longitudes, [5]; Appendix C. Data for profiles, [6]–14.

Volume VI — 1857

33d Cong., 2d Sess., Senate Ex. Doc. No. 78 [Serial No. 763]

The title-page of *Pacific Railroad Reports*, Volume VI, is dated 1857. This date is corroborated in a footnote to "Contents" of Abbot's zoological report, (Volume X, [7]), which reads: "Numbers 1, 2, and 3 [of Part IV. Zoological report, my (4) below] will be found in Vol. VI of the Pacific Railroad Surveys, printed and published in 1857 . . ."

Volume VI has five sets of page numbers.

The title-page covering the content of Volume VI reads:

Report of Lieut. Henry L. Abbot, Corps of Topographical Engineers, upon explorations for a railroad route, from the Sacramento Valley to the Columbia River, made by Lieut. R. S. Williamson, Corps of Topographical Engineers, assisted by Lieut. Henry L. Abbot, Corps of Topographical Engineers.

CONTENTS (front matter): Letter to the Secretary of War,[29] [3]–4; General table of contents, [5]; Introduction. Instructions from the War Department, [7]–15.

The Abbot report has five main subdivisions, distinguished here as (1), (2), (3), (4) and (5). Their respective title-pages read:

(1) Part I. General report. [17]–134. 12 plates (Nos. I–XI, XIII). 3 woodcuts.

CONTENTS: Contents, [21]–23; List of illustrations, [24]; General report (7 chapters), [25]–129; Index to General report, [130]–134.

For maps and profiles *see* under Volume XI.

(2) Part II. Geological report, [1]–85.

CONTENTS: Contents, [5]–7; List of illustrations, [8]; Nos. 1, 2, 3, and 4 of Geological report, [9]–85.

Part II contains four papers, headed respectively:

No. 1. Report upon the geology of the route. By J. S. Newberry, M.D., Geologist of the expedition (8 chapters), [9]–68. 1 plate (No. I). 11 woodcuts.

No. 2. Description of the tertiary fossils collected on the survey. By T. A. Conrad. [69]–73. 4 plates (Nos. II–V).

No. 3. Report upon an analytical examination of water and

Reptiles, by Dr. Edward Hallowell"; "No. 4 Fishes, by Dr. Charles Girard." For these papers *see* under Volume X.

[29] The Hon. Jefferson Davis held the post of Secretary of War from March, 1853, to March, 1857. The letter is addressed to the Hon. John B. Floyd who had been appointed to that office by President Buchanan in March, 1857.

minerals from the Hot Springs in Des Chutes Valley. Conducted under the direction of Prof. E. N. Horsford.[30] [74]–78.

No. 4. Catalogue of the minerals and fossils collected on the survey. [79]–85.

(3) Part III. Botanical report. [1]–102.

CONTENTS: Contents, [5]; List of illustrations, [7]–8; Nos. 1 and 2 of Botanical report, [9]–94; Index to Botanical report, [97]–102.

For plates and woodcuts *see* under Nos. 1 and 2 below.
Nos. 1 and 2 are headed respectively:

No. 1. Report upon the botany of the route. By John S. Newberry, M.D., Botanist of the expedition (2 chapters), [9]–64.
Chapter I. Geographical botany. [9]–19.
Chapter II. Description of the forest trees of northern California and Oregon. [20]–64. 10 plates (Nos. I–X). 28 woodcuts.

No. 2. General catalogue of the plants collected on the expedition. By J. S. Newberry, assisted by Asa Gray and John Torrey, as specified in the proper places, [65]–94.

No. 2 has four subdivisions:

I. Exogenous plants.[31] [65]–90. 6 plates (Nos. XI–XVI).
II. Endogenous plants. By John Torrey, [90]–92.
III. Mosses and liverworts. By W. S. Sullivant, 93–94.
IV. Lichens. By Edward Tuckerman, 94.

(4) Part IV. Zoological report. [1]–114.

CONTENTS: Contents, [5]; List of illustrations, [6]; Prefatory note to Part IV, [7]; Nos. 1, 2, and 3 [32] of Zoological report, [9]–114; Index to Zoological report, [i]–iv.

The subdivisions included in the Zoological report are the following:

No. 1. Report upon fishes collected on the survey. By Charles Girard, M.D. [9]–34. 11 plates. (Nos. XXIIa, XXIIb, XXVa, XXVb, XLa, XLVI, LXII, LXVI, LXVIII, LXX, LXXIV).

No. 2. Report upon the zoology of the route. By J. S. Newberry, M.D.[33] (2 chapters), [35]–110.

For allocation of included plates *see* under Chapters I, II, below.
The chapters are headed:

[30] A Horsford letter, [74], refers to this as ". . . the report of my assistant, Mr. L. M. Dornbach. . ."

[31] In "Contents," [5], of Botanical report, the authors of "Exogenous plants" are named as Asa Gray, John Torrey, and J. S. Newberry.

[32] For omission of Part IV, No. 4, which had been cited in "Contents," [5], *see* "*Note*" following No. 3 below.

[33] A *fn.*, [38], states: "The species enumerated in this report have been determined, and their diagnoses prepared, by Prof. S. F. Baird, Assistant Secretary of the Smithsonian Institution."

Chapter I. Report upon the mammals: [35]–72. 3 plates (Nos. I, III, XXII).

Chapter II. Report upon the birds.[34] [73]–110. 2 plates (Nos. XXVI, XXXIV.

No. 3. Report upon the land shells collected on the survey. By W. G. Binney, Member of the Academy of Natural Sciences of Philadelphia. [111]–114.

A "Note" on an inserted page, following p. 114, states: "*No. 4 has not been completed in time for publication with the rest of this Report. It will appear in a subsequent volume.*" No. 4 had been cited in the "Contents," [5], of Part IV. Zoological report as: "Report upon reptiles collected on the survey. By S. F. Baird, Assistant Secretary of the Smithsonian Institution." For this *see* under Volume X.

(3) Appendices. [1]–64.

Distinguished by letters A through F, these 13 Appendices relate to astronomical observations and the like. They are enumerated in "General table of contents," [5], of the Abbot report.

An inserted page following the Appendices lists "Errata for Volume VI."

Volume VII — 1857

33d Cong., 2d Sess., Senate Ex. Doc No. 76 [Serial No. 764]

The title-page of *Pacific Railroad Reports*, Volume VII, is dated 1857. No included matter bears a later date.

Volume VII has five sets of page numbers.

"Contents of Volume VII," [3], records two subdivisions, distinguished here as (1) and (2). The title-page of the first reads:

(1) Report of explorations for railroad routes from San Francisco Bay to Los Angeles, California, west of the Coast Range, and from the Pimas Villages on the Gila to the Rio Grande, near the 32d parallel of north latitude, by Lieutenant John G. Parke, Corps of Topographical Engineers, assisted by Albert H. Campbell, Civil Engineer.

CONTENTS: Letter to the Secretary of War, (7); General table of contents, [9]; Introduction. Instructions from the War Department, [11]–15; Part. I. General report, [17]–[23],[35] [1]–12; Part II. Geological report, [1]–204; Part III. Botanical report, [1]–28; Appendices (A through E), [1]–118.

[34] A *fn.*, [73], reads: "As the final determination of the species of birds collected by the expedition has not yet been completed by Prof. Baird, the names here given are to be considered as temporary. In his general report upon the birds of the Pacific Railroad Surveys, hereafter to appear, the names and pages of the species in this article will be carefully quoted, and any errors of determination thus rectified." For Baird's "general report upon the birds" see under Volume IX.

[35] The 23 pages (8 blank) which precede the text proper of Part I. General report, are, with the exceptions of pages 14, 15, 22, unnumbered. The content of some relate to Parke's report as a whole, while others represent front matter to Part I. I have inserted the missing page numbers and have allocated the subject matter to accord with my understanding of its proper association.

For maps and profiles *see* under Volume XI.

Parts I, II, III, and Appendices are cited on their respective title-pages as follows:

Part I. General report. [17]–[23]; [1]–42. 8 plates.

For allocation of the plates *see* under Nos. 1 and 2 below. For maps and profiles *see* under Volume XI.

CONTENTS: Contents, [21]–[23]; [1]–23; List of illustrations, [23]; Nos. 1 and 2, [1]–42.

The two subdivisions of the General report are headed:

No. 1. Report of explorations from San Francisco Bay to Los Angeles. [1]–18. 3 plates (Nos. I, II; the third not numbered).

No. 2. Report of explorations from Pimas Villages to Rio Grande. [19]–42. 5 plates (Nos. VI [= IV], V, VI, VII, VIII).

Part II. Geological report, by Thomas Antisell, M.D., Geologist of the expedition. [1]–204. 2 maps (geological). 24 plates.

For allocation of plates *see* under Chapters XXIX and XXX below.

CONTENTS: Contents, [5]–10; List of illustrations, [11]–13; Geological report (30 chapters), [15]–197; Description of the plates, [19]–204.

Of the 30 chapters of the Geological report, Chapter XXIX ("Report upon the palaeontology of the survey. By T. A. Conrad"), [189]–196, contains 10 plates (Nos. I–X); and Chapter XXX ("Order of position of Californian strata"), [197], contains 14 plates (Nos. I–XIV).

Part III. Botanical report: by John Torrey. [1]–28. 8 plates.

For allocation of plates *see* under Chapter I below.

CONTENTS: Contents,[36] [5]; Chapters I, II, III, [7]–28.

The subdivisions of the Botanical report are headed respectively:

Chapter I. List and descriptions of the plants collected. By John Torrey, M.D. [7]–22. 8 plates (Nos. I–VIII).

Chapter II. Synoptical tables of botanical localities. By Thomas Antisell, M.D. [23]–26.

Chapter III. Description of the plates. By John Torrey, M.D. [27]–28.

Appendices. [1]–116. 11 plates.

For allocation of plates *see* under Appendix A.

The five Appendices are headed respectively:

Appendix A. Remarks on meteorology and barometic results, with meteorological plates. By Albert C. Campbell, A.M. Civil Engineer to the expedition. [3]–14. 11 plates (Nos. I–XI).

Appendix B. Report upon the route from San Diego to Fort

[36] This contains a list of plates.

Yuma via San Diego River, Warner's Pass, and San Felipe Canon. By Charles M. Poole, Chief Engineer. [15]–28.

Appendix C. Translation of an archive from Tucson. [29]–30.

Appendix D. Description of maps and profiles, with table of latitudes. [31]–34.

Appendix E. Table of distances, and barometric and meteorological observations and results. By Albert H. Campbell, A.M., Civil Engineer to the expedition. 35–116.

The title-page of the second subdivision of Volume VII reads:

(2) Conclusion of the official review of the reports upon the explorations and surveys for railroad routes from the Mississippi River to the Pacific Ocean. [1]–37.

For General map and General profiles *see* under Volume XI.

CONTENTS: Contents, [3]; Prefatory note, [5]; Nos. 1, 2, 3, 4, 5, [7]–37.

The five subdivisions of the "official review" are headed respectively:

No. 1. Extract from the annual report of the Secretary of War. December, 1855. [7]–10.

No. 2. Report upon the progress of the Pacific Railroad explorations and surveys. November, 1855. By Captain A. A. Humphreys, Corps of Topographical Engineers. [11]–18.

No. 3. Extract from the annual report of the Secretary of War, December, 1856. [19]–22.

No. 4. Report upon the progress of the Pacific Railroad explorations and surveys. November, 1856. By Captain A. A. Humphreys, United States Topographical Engineers. [23]–34.

No. 5. Table exhibiting the comparative lengths, cost, etc., of the different routes, with explanatory remarks. By Captain A. A. Humphreys, Corps Topographical Engineers. [35]–37.

Volume VII ends with an inserted page: "Errata for Volume VII."

Volume VIII — 1857

33d Cong., 2d Sess., Senate Ex. Doc. No. 79 (Serial No. 765)

The title-page of *Pacific Railroad Reports*, Volume VIII, is dated 1857. This date is corroborated in the "Preface" to Part II. Birds (Volume IX, [xiii]) which refers to the account of the mammals (Part I. below) as ". . . having been published in 1857. . ."

The pages of Volume VIII are numbered consecutively throughout.

Following "Contents of Volume VIII," [iii], is a title-page reading:

General report upon the zoology of the several Pacific Railroad routes.

CONTENTS: Letter to Captain Humphreys, Topographical Engineers,

[vii]; General table of contents,[37] [ix]; Introduction. General sketch of lines explored,[38] [xi]–xvii.

The title-pages covering the content of Volume VIII read:

Part I. Mammals: by Spencer F. Baird, Assistant Secretary of the Smithsonian Institution. [xix]–xlviii; [1]–757. 38 woodcuts. 43 plates. (Nos. XVII–XXVIII, XXX–LX).

CONTENTS: Contents, [xxiii]; Preface, [xxv]–xxix; Table of the higher groups, xxx–xxxi; List of species, [xxxii]–xlviii; Introductory remarks, [1]; [Orders of mammals, I through VI], [3]–684; Appendix A. List of authorities referred to in the preceding report, [685]–703; Appendix B. Alphabetical list of localities referred to in the preceding report, [704]–715; Alphabetical index. I. Systematic index of common names, [717]–720; Alphabetical index. II. Systematic index of scientific names, [721]–735; Explanation of the plates,[39] [737]–750; List of wood-cut figures, 750–752; Systematic list of illustrations, 755–757.

Volume IX — 1858

33d Cong., 2d Sess., Senate Ex. Doc. No. 78 [Serial No. 766]

The title-page of *Pacific Railroad Reports*, Volume IX, is dated 1858. No included matter bears a later date.

The pages of Volume IX are numbered consecutively throughout.

It is a continuation of the "General report upon the zoology of the several Pacific Railroad routes" begun in Volume VIII.

Following "Contents of Volume IX," [iii], and "Letter to Captain Humphreys, Topographical Engineers," [v], are title-pages readings:

Part II. Birds: by Spencer F. Baird. Assistant Secretary Smithsonian Institution. With the co-operation of John Cassin and George N. Lawrence. [vii]–lvi; [1]–1005.

CONTENTS: Contents, [xi]; Preface,[40] [xiii]–xvi; I. Table of the

[37] This cites the content of Volume VIII (Part I. Mammals); of Volume IX (Part II. Birds); and of Volume X (as to Part III. Reptiles and Part IV. Fishes).

[38] A valuable reference paper, enumerating collectors in natural history, not only along the main lines of the Pacific Railroad surveys but along routes "intimately connected" therewith. Included also are men who, working independently, made collections contributing to the report. For a somewhat similar paper *see* "Preface" (Volume IX, [xiii]–xvi).

[39] A *fn.*, [747] explains to which reports the plates of mammals enumerated in the list of illustrations supplied in the "Explanation of the plates" should be allocated: whether to the "General report upon the zoology of the several Pacific Railroad routes" (" . . . all that have been prepared for the present volume . . .") or to ". . . the special reports of the different railroad parties. . .", and tells how plates associated with special reports should be distinguished. A list of officers in command of the different lines of survey and the zoologists associated with them, is also supplied. Despite the explicit directions, attempts to check the plates were not successful.

[40] This useful enumeration of collectors is somewhat similar to the one supplied in "Introduction. General sketch of lines explored" (Volume VIII, [xi]–xvii) for the reason that some of the men collected in more than one branch of natural history. But it contains additional names and covers some different territory.

higher groups, [xvii]–xxiv; II. List of species, [xxx]–lvii; Introductory remarks, [1]–2; [Orders of birds, I through VI], [3]–920; Appendix A. Additional remarks on North American birds, [921]–925; Appendix B. Birds found at Fort Bridger, Utah, [926]–937; Appendix C. List of authorities referred to in the preceding report, [928]–954; Alphabetical index. I. Systematic index of common names, [955]–963; Alphabetical index. II. Systematic index of scientific names, [965]–1005.

Volume X — 1859

33d Cong., 2d Sess., Senate Ex. Doc. No. 78 [Serial No. 767]

The title-page of *Pacific Railroad Reports*, Volume X, is dated 1859. This date is corroborated in a footnote to the "Contents" of Abbot's report (Part IV. Zoological report, Volume X, [7]), which states: "No. 4 [Report on reptiles collected on the survey. By S. F. Baird] dates 1859." *See fn.* 49.

Volume X has seven sets of page numbers.

"Contents of Volume X," [3], names two subdivisions: first, Parts III and IV of the "General report upon the zoology of the several Pacific Railroad routes" (continued from Volumes VIII and IX); and, second, five groups of zoological papers which had not been ready when the reports with which they are affiliated has been published; they are distinguished here as (1), (2), (3), (4), and (5).

The title-pages of Parts III and IV read respectively:

Part III. Reptiles: by Spencer F. Baird, Assistant Secretary of the Smithsonian Institution. [7]–18. 13 plates (Nos. XXIV–XXXVI).

CONTENTS: Letter of Humphreys,[41] [11]; Explanation of the plates, [13]–16.

Part IV. Fishes: by Charles Girard, M.D. [i]–xiv; [1]–400. 21 plates (Nos. VII, VIII, XIII, XIV, XVII, XVIII, XXIIc, XXVI, XXIX, XXX, XXXIV, XXXVII, XL, XLI, XLVIII, LIII, LIX, LXI, LXIV, LXV, LXXI).

CONTENTS: Contents, [v]–xiv; Introductory remarks,[42] [1]–2; [Orders of fishes, I through X], [3]–284; List of the plates,[43] [385]–388; Alphabetical index, 389–400.

The title-pages of the five groups of reports forming the second subdivision of Volume X read respectively:

(1) Report of Lieut. E. G. Beckwith, Third Artillery, upon explorations for a railroad route, near the 38th and 39th parallels of north latitude,

[41] This reads: "The General Natural History Reports having been extended so much beyond the limits originally contemplated, the War Department has considered it advisable to omit the publication of the Report on Reptiles. The plates to accompany this report having been prepared and printed, they, with a brief explanation of the figures composing them, are herewith given."

[42] These appear in two forms in the printing under analysis. One was presumably a preliminary draft and should have been omitted.

[43] A *fn.* states: "Plates XXIIa, XXIIb, XXVa, XLa, XLVI, XLVII, LXVI, LXVIII, LXX and LXXIV of this list will be found in vol. VI, part IV, of the present series. Other plates missing from this volume will be found in vol. X."

by Captain J. W. Gunnison, Corps of Topographical Engineers, and near the forty first parallel of north latitude, by Lieut. E. G. Beckwith, Third Artillery. Zoological report.[44] 20 plates.

For allocation of the plates see under Nos. 1, 2, 3, and 4 below.

CONTENTS: Contents,[45] [5], List of illustrations, [6]; Nos. 1, 2, 3, and 4, [7]–27; Alphabetical index, [28].

The four included zoological reports are headed respectively:

No. 1. Report upon mammals collected on the survey. By S. F. Baird. [7]–9. 3 plates (Nos. IV, VI, X).

No. 2. Report upon birds collected on the survey. By S. F. Baird. [13]–16. 7 plates (Nos. XII, XIII, XIV, XV, XVII, XXXII, XXXV).

No. 3. Report on reptiles collected on the survey. By S. F. Baird. [17]–20. 4 plates (Nos. XVII, XVIII, XXIII, XXIV).

No. 4. Report on fishes collected on the survey. By Charles Girard, M.D. [21]–27. 6 plates (Nos. XXIII, XLIX, LIV, LVI, LXXIII, LXXV).

(2) Report of explorations for a railway route (near the thirty-fifth parallel of north latitude), from the Mississippi River to the Pacific Ocean. By Lieutenant A. W. Whipple, Corps of Topographical Engineers: assisted by Lieutenant J. C. Ives, Corps of Topographical Engineers. Part VI.[46] Zoological report. [1]–34. 34 plates.

For allocation of plates *see* under Nos. 2, 3, 4 and 5 below.

CONTENTS: Contents,[47] [7]; List of illustrations, [9]–10; Nos. 2, 3, 4, and 5, [11]–59; Alphabetical index, [61]–64.

The four included zoological reports are headed respectively:

No. 2. Report on mammals collected on the survey. By C. B. R. Kennerley, M.D. [11]–18. 6 plates (Nos. VIII, XI, XII, XIII, XIV, XVI).

No. 3. Report on birds collected on the route. By C. B. R. Kennerley, M.D. [19]–35. 11 plates (Nos. XVIII, XIX, XX, XXII, XXVII, XXIX, XXX, XXXI, XXXIII, XXXVI, XXXVII).

[44] A *fn.* states: "The report to which this article belongs will be found in Vol. II of this series."

[45] Of five zoological reports listed, only four are included. The missing report, named in "Contents" as "No. 5. Report on insects collected on the survey. By John L. Leconte, M.D.," has not been found in the quarto series.

[46] For Parts I, II, III and IV, *see* Volume III; for Part V, and Part VI, No. 1, *see* Volume IV.

[47] Of five zoological reports cited, only four are included. Of the missing report (No. 1. Field notes and explanations. By C. B. R. Kennerley, M.D.) it is stated in a *fn.*: "No. 1 has already appeared in Vol. IV, 1856." According to my analysis Volume IV was published in 1857, certainly not earlier. See Volume IV, Introduction to Part V, No. 4, [59], which is dated January 12, 1857.

No. 4. Report upon the reptiles of the route. By S. F. Baird. [37]–45. 3 plates (Nos. XXV, XXVI, XXVII).

No. 5. Report upon fishes collected on the survey. By C. Girard, M.D. [47]–59. 14 plates (Nos. III, IV, V, VI, IX, X, XXI, XXIV, XXV, XXXV, XLb, LII, LVII, LVIII).

(3) Report of explorations for a railroad route near the 32d parallel of north latitude, lying between Dona Ana, on the Rio Grande, and Pimas Villages, on the Gila, by Lieutenant John G. Parke, Corps of Topographical Engineers. Zoological report. [1]–24. 4 plates.

For allocation of plates *see* under Nos. 1 and 2 below.

CONTENTS: Contents, [5]; List of illustrations, [6]; Introductory letter, [7]; Nos. 1 and 2, [9]–24.

The two included zoological reports are headed respectively:

No. 1. Report upon the birds collected on the survey. By A. L. Heermann, M.D. [9]–21. 3 plates (Nos. I, IV, VI).

No. 2. Report upon reptiles collected on the survey. By Edward Hallowell, M.D. [23]–24. 1 plate (No. II).

(4) Report of explorations in California for railroad routes to connect with the routes near the 35th and 32d parallels of north latitude. By Lieutenant R. S. Williamson, Corps of Topographical Engineers. Part IV. Zoological report, [i]–[viii]; [1]–91. 26 plates.

For allocation of plates *see* under Nos. 1, 2, and 4 below.

CONTENTS: List of illustrations, [vi]; Contents,[48] [vii]; Introductory letter. By A. L. Heermann, M.D. [viii]; Nos. 1, 2, 3 and 4, [1]–91; Alphabetical index, [93]–97.

The four included zoological reports are headed:

No. 1. Report upon the reptiles collected on the survey. By Dr. Edward Hallowell. [1]–23; List of reptiles collected. By Dr. A. L. Heermann, Naturalist to the expedition, [24]–25; Explanation of the plates, [26]–27. 9 plates (Nos. I, III, IV, V, VII, VII [sic], VIII, IX, X).

No. 2. Report upon birds collected on the survey. By A. L. Heermann, M.D. [29]–77; List of birds collected between San Francisco and Fort Yuma, California, during the survey of railroad routes from the Mississippi to the Pacific Ocean, under the command of Lieutenant R. S. Williamson, Top. Engs. [79]–80. 7 plates (Nos. II, III, V, VII, VIII, IX, X).

No. 3. Report on mammals collected on the survey. By S. F. Baird. [81]–82.

No. 4. Report on fishes collected on the survey. By Charles Girard,

[48] A *fn.* states: "The report to which the present part belongs will be found in volume V."

M.D. [83]–91. 10 plates (Nos. II, XII, XXII, XXVII, XXVIII, XXXI, XXXVI, XXXVIII, XXXIX, XLVII).

(5) Report of Lieut. Henry L. Abbot, Corps of Topographical Engineers, upon explorations for a railroad route, from the Sacramento Valley to the Columbia River, made by Lieut. R. S. Williamson, Corps of Topographical Engineers, assisted by Lieut. Henry L. Abbot, Corps of Topographical Engineers. Part IV. Zoological report. [1]–13. 4 plates.

For plates *see* under No. 4 below.

CONTENTS: Contents,[49] [7]; List of illustrations, [8]; No. 4, [9]–15.

The included zoological report is headed:

No. 4. Report on reptiles collected on the survey. By S. F. Baird. [9]–13. 4 plates (Nos. XI, XXVIII, XXX, XLIV).

Volume XI — 1859

33d Cong., 2d Sess., House Ex. Doc. No. 91 [Serial No. 801]

The title-page of *Pacific Railroad Reports*, Volume XI, is dated 1855, but the title-page of Warren's Memoir as well as the title-page preceding the maps, profiles, plates, etc., which form the last half of the volume, are dated 1859.

Following the "Contents of Volume XI," [3], and "Letter to the Secretary of War," [5], is a title-page reading:

Memoir to accompany the map of the territory of the United States from the Mississippi River to the Pacific Ocean, giving a brief account of each of the exploring expeditions since A.D. 1800, with a detailed description of the method used in compiling the general map. By Lieut. Gouverneur K. Warren, Corps of Topographical Engineers, U.S.A. [3]–120. 4 plates (Nos. I, II, III, IV).[50]

CONTENTS: Letter to Captain A. A. Humphreys, Topographical Engineers, [9]; Contents, [11]–12; List of illustrations, [13]; Introductory remarks, [13]–16; Memoir (6 chapters), [17]–115; Alphabetical index, [117]–120.

The remainder of Volume XI is preceded by a title-page reading:

Topographical maps, profiles, and sketches, to illustrate the various reports of surveys for railroad routes from the Mississippi River to the Pacific Ocean.

This is followed by "Contents," [iii]–iv, in which the illustrations, segregated under ten headings, are meticulously enumerated and described. These headings and the total number and type of illustration allotted to each in the "Contents" follow:

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[49] A *fn.* states: "Numbers 1, 2, and 3 will be found in Vol. VI of the Pacific Railroad Surveys, printed and published in 1857. No. 4 dates 1859."

[50] These are reduced copies of old maps, intended for insertion in the text.

Sketch of route of the 41st parallel — Beckwith's Report, Vol. II. 8 plates (views). 5 panoramas (views).

Official review of the reports — Vols. I and VII. General map. General profile.

Route of the 47th and 49th parallels — Stevens's Report, Vol. I. 3 maps (Nos. 1, 2, 3). Profiles.

Routes in Oregon and California — Abbot's Report, Vol. VI. 2 maps (Nos. 1, 2). 2 profiles (Nos. 1, 2).

Route near the 41st parallel — Beckwith's Report, Vol. II. 4 maps (Nos. 1, 2, 3, 4). Profiles of the route.

Route near the 38th and 39th parallels — Beckwith's Report, Vol. II. Profiles of the route. 4 maps (Nos. 1, 2, 3, 4).

Route near the 35th parallel — Whipple's Report, Vol. III. 2 maps (Nos. 1, 2). Profiles.

Routes in southern California — Williamson's Report, Vol. V. 4 maps. 2 profiles (sheets Nos. 1, 2).

Routes in California and on the 32d parallel — Parke's Reports, Vol. VII. 2 maps (Nos. 1, 2). Profiles.

Route of the 32d parallel — Pope's Report, Vol. II. Map and profile.

Volume XII. Book I [51] — 1860

36th Cong., 1st Sess., House Ex. Doc. No. 56 [Serial No. 1054]

The title-page of *Pacific Railroad Reports*, Volume XII, Book I, is dated 1860. No included matter bears a later date.

The volume has two sets of page numbers.

"Contents of Volume XII. Book I," [3], records two subdivisions: Part I and Appendices.[52]

Following "Contents of Volume XII. Book I" is a title-page reading:

Narrative and final report of explorations for a route for a Pacific railroad, near the forty-seventh and forty-eighth parallels of north latitude, from St. Paul to Puget Sound. By Isaac I. Stevens, Governor of Washington Territory.

This is followed by "Letter to the Secretary of War," by the "General table of contents" and by an "Introduction."

[51] The first Stevens report appeared in Volume I. His second and final report and the scientific papers associated with it necessitated two volumes which are distinguished on the title-pages of *Pacific Railroad Reports* as "Volume XII. Book I" and "Volume XII. Book II."

[52] The subdivisions are in accord with the contents of Book I as issued. For the reason that, with one exception, none of the pages in Volume I preceding page 20 is numbered and the exception, page "18," bears no numerical relationship to those which precede or follow it, and for the reason that the "General table of contents," [9], places the Appendices after Part III. Zoological report (Volume XII. Book II), it seems probable that there were "last minute" changes in the compilation of Books I and II which were not incorporated in the introductory pages of Book I. *See* also *fn.* 54.

The title-page of the first subdivision of Volume XII, Book I reads:

Part I. General report. [15]–358. 70 plates (Nos. I–LXX). 2 maps. 1 sheet of profiles.

CONTENTS: Contents, [19]–27; List of illustrations, [29]–30; General report (18 chapters), [31]–358.[53]

The second subdivision of Volume XII. Book I is preceded by a title-page reading:

Appendices. [1]–25.[54]

CONTENTS: Appendix A. Heights and distances. [3]–12; Appendix B. Meteorological register, [13]–25.

Volume XII. Book II — 1860

36th Cong., 1st Sess., House Ex. Doc. No. 56 [Serial No. 1055]

The title-page of *Pacific Railroad Reports*, Volume XII. Book II, is dated 1860. No included matter bears a later date.

The volume has two sets of page numbers.

It is a continuation of the Stevens report begun in Volume XII. Book I. "Contents of Volume XII. Book II," [3], divides the subject matter into two Parts which are cited on their respective title-pages as follows:

Part II. Botanical report. [5]–76. 6 plates.

For allocation of plates *see* under Nos. 2 and 3 below.

CONTENTS: Contents, [9]; List of illustrations, [11]; Nos. 1, 2 and 3 of Botanical report, [13]–71; Index to Botanical report, [73]–76.

The three included papers are headed respectively:

No. 1. Report on the botany of the route. By J. G. Cooper, M.D. [13]–39.

No. 2. Catalogue of plants collected east of the Rocky Mountains. By Professor Asa Gray. [40]–49. 5 plates (Nos. I, II, III, IV, V).

No. 3. Catalogue of plants collected in Washington Territory. By J. G. Cooper, M.D. [50]–71. 1 plate (No. VI).

Part III. Zoological report. [i]–[ix]; [1]–399. 46 plates.

For allocation of plates *see* under Nos. 1, 2, 3, 4, 5 below.

CONTENTS: Contents, [v]–vi; List of illustrations,[55] [vii]–viii.

[53] The "General report" is subdivided into Narrative of 1853 (Chapters I–X, [31]–195); Narrative of 1855 (Chapters XI–XII, [196]–225); Geographical memoir (Chapters XIII–XVI, [226]–331); Railroad report and estimate (Chapter XVII, [332]–351); Computation of altitudes from barometrical observations. Table of heights and distances. Meteorological register (Chapter XVIII, [352]–358).

[54] Following the Appendices and with pages in numerical sequence thereto is an Alphabetical index, [27]–41. Its content does not cover the Appendices and its existence is nowhere recorded in the volume. *See fn.* 52.

[55] This enumerates between 80 and 90 plates, more than half of which are referred to zoological reports contained in Volume XII. Book II, and the remainder to zoological reports published in earlier volumes of the series. Attempts to check the enumeration

Prefatory note to Part III, [ix]; Nos. 1 through 7 of Zoological report, [1]–389; Index to Zoological report, [391]–399.

Part III contains 7 papers, headed respectively:

No. 1. Report upon insects collected on the survey. By John T. Leconte, M.D. [1]–77. 2 plates (Nos. I, II).

No. 2. Report upon the mammals collected on the survey. [73]–138. 5 plates.

For allocation of plates *see* under Chapters I and II below.

No. 2 contains 3 reports headed respectively:

Chapter I. Report by J. G. Cooper, M.D. [73]–88. 4 plates (Nos. V, VII, IX, XV).

Chapter II. Report by Dr. Geo. Suckley, U.S.A. [89]–106. 1 plate (No. II).

Chapter III. Report of Dr. Geo. Suckley, U.S.A., and Geo. Gibbs, Esq. [107]–138.

No. 3. Report upon the birds collected on the survey. [140]–291. 8 plates.

For allocation of plates *see* under Chapters I, II, below.

No. 3 contains 2 subdivisions, headed respectively:

Chapter I. Land birds, by J. G. Cooper, M.D. [140]–226. 7 plates (Nos. XI, XVI, XXVIII, XXI, XXIII, XXIV, XXV).

Chapter II. Water birds, by Dr. G. Suckley, US.A. [227]–291. 1 plate (No. XXXVIII).

No. 4. Report upon the reptiles collected on the survey. By J. G. Cooper, M.D. [292]–306. 11 plates. (Nos. XII, XIII, XIV, XV, XVI, XIX, XX, XXI, XXII, XXIX, XXXI).

No. 5. Report upon the fishes collected on the survey. By Dr. G. Suckley, U.S.A. [307]–368. 21 plates (Nos. I, XI, XV, XVI, XIX, XX, XXXII, XXXIII, XLII, XLIII, XLIV, XLV, L, LI, LV, LX, LXIII, LXVII, LXIX, LXXII, LXXV).

No. 6. Report upon the Mollusca collected on the survey. By William Cooper. [369]–386.

No. 7. Report on the Crustacea collected on the survey. By J. G. Cooper, M.D. [387]–389.

ALPHABETICAL INDEX OF AUTHORS TO BE USED IN CONJUNCTION WITH THE ANALYSES [56]

ABBOT, H. L. (Sacramento Valley to Columbia River): Report, v. VI.
AGASSIZ. L. (Williamson route): Fossil fishes, v. VI.

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of this List with plates in the given reports have not been satisfactory, either as to the total number of plates or as to their allocation. *See fn.* 39.

[56] To the first Stevens report published in Volume I are appended (pp. 160–635),

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together with letters, etc., etc., a number of signed documents describing work done in connection with particular sections and aspects of his survey; some of these (pp. 160–449) were appended to the report when submitted; others (pp. 449–635) were added at a later date. In my analysis of the content of the report these papers are merely noted as "Miscellaneous documents related to special aspects of the survey, 160–635", and neither the authors nor the long descriptive titles of their papers are enumerated — in *fn.* 10, reference is made to the present statement.

In the "Alphabetical index of authors" the names of those who contributed these appended papers are preceded by an asterisk and the pages where their contributions appear in the Stevens report of Volume I are supplied. In instances where authors contributed papers which are cited in the analyses, and appended reports also, the first take precedence and the last are preceded by the notation *See also*.

STUDIES IN THE GENUS COCCOLOBA, VI. THE SPECIES FROM THE LESSER ANTILLES, TRINIDAD AND TOBAGO *

RICHARD A. HOWARD

THE PRESENT STUDY continues a series of papers on the genus *Coccoloba* as it occurs in the West Indies. A single study of the genus as a whole has been considered impossible for a number of reasons. Not only is the genus a large one, but reliable data based on field observations, particularly in relation to hybridity and possible apomixis, have been lacking. In addition, the application of many names is difficult, for too many species, including some only recently described, have been based on anomalous specimens (adventitious shoots, for example). Many names either have been misapplied or have passed unnoticed and many species are represented only by the type collection. A further difficulty is the lack of strong and easily defined characteristics which can be used in dividing the genus taxonomically. Some of these obstacles have been overcome in part, as has been pointed out in earlier papers of this series. However, other difficulties, such as our inadequate knowledge of the range of variation in these plants, still remain and much more field work will be needed.

The artificial geographical division which was the basis for my previous studies of the genus as it occurs in Cuba, Jamaica, Puerto Rico and the Bahamas, Hispaniola, and now the Lesser Antilles and Trinidad, has allowed progressive steps which will be the foundation for further work on the genus in South America, Central America and Mexico.

In 1950 I completed a field study of *Coccoloba* in the Lesser Antilles, Trinidad and Tobago which supplied much of the material and information used in this paper. I am grateful to the directors of the American Philosophical Society and the directors of the Milton Fund of Harvard University for grants which made the field work possible. Specimens used in this study have been borrowed from a number of herbaria and botanical institutions represented by the standard abbreviations given. I wish to express my grateful appreciation to the directors and the curators of these institutions for the use of these specimens.

The same difficulties encountered in earlier work apply to this study. Although field work in the Caribbean area has resolved many problems, many others remain and further studies will be necessary for a complete understanding of many of the species. The variation in leaf-form and -size when correlated with the growth habit of any particular plant should be incorporated into a general description of the species. In doing so, the

*The preceding papers in this series will be found in Jour. Arnold Arb. **30**: 388–424. 1949; **37**: 317–339. 1956; **38**: 81–106. 1957; **38**: 211–242. 1957; **39**: 1–48. 1958.

construction of a key to species to cover all variations seen in the field and represented in the herbarium collections becomes more difficult. In some species only one sex is known; in some, the fruiting material is unknown or is inaccurately associated with the flowering material.

Fortunately, I have been able to see the type material of all of the more recently described species and all but a few of the older species. Many of Lindau's species from Trinidad were based on specimens in the herbarium of the Imperial College of Tropical Agriculture, Port of Spain, Trinidad. Fragments of these specimens were placed by Lindau in the herbarium of Krug and Urban in the Botanisches Museum in Berlin. The fragments remain in Berlin, but the more complete material in Trinidad has largely been destroyed by the tropical environment and by periods of neglect.

The geographic area considered in this paper is currently regarded as an unnatural one. The Lesser Antilles (the Leeward and Windward Islands from Antigua to Grenada) form a group of relatively young islands, mostly volcanic in origin. The natural vegetation of this area is presumed to have been derived by migrations southward from the Greater Antilles, by migrations northward from Trinidad and South America and by the *in situ* development of some endemic or localized species. Trinidad and Tobago, in contrast, appear floristically as well as geologically as a part of the South American mainland. Of the seventeen taxa considered in this paper, two (*Coccoloba uvifera* and *C. venosa*) are widespread, appearing along the seacoasts of the Antilles, Central America and South America. Four species and one form, *C. diversifolia*, *C. krugii*, *C. pubescens*, *C. swartzii* and *C. swartzii* f. *pubescens*, are found in the Greater Antilles and extend to varying degrees into the Lesser Antillean islands. Only one taxon, *C.* × *boxii*, representative of a hybrid population, occurs only in the Lesser Antilles. *Coccoloba dussii* occurs only in the Lesser Antilles and Trinidad, but is very similar to a species from South America. *Coccoloba ascendens* and *C. novogranatensis* occur in the Lesser Antilles and Trinidad and in South America, with the range of *C. novogranatensis* extending west and then north through Central America, while the range of *C. ascendens* continues south and east in Brazil. Five species (*C. cruegeri*, *C. fallax*, *C. latifolia*, *C. nitida* and *C. striata*) occur in Trinidad and South America but have not been found in the Lesser Antilles. One species, *C. nigrescens*, is currently known only from the Bocas Islands near Trinidad, but additional material will probably reveal its relationship or identity with other southern species.

Thus, in contrast to the Greater Antilles where the genus *Coccoloba* has evolved a great many endemic species, neither Trinidad nor the Lesser Antilles has experienced a parallel elaboration of the genus. The Lesser Antillean species of *Coccoloba* are predominantly Greater Antillean species which have migrated southward. The species found in Trinidad are basically South American and only a few species have migrated northward into the Lesser Antilles.

Following the key, the species are described and are listed in alphabetical order.

KEY TO THE SPECIES

A. Inflorescence paniculate, stems thick, striate-angled, hollow; leaves umbonate between the conspicuously reticulate veins. ..... *C. latifolia.*

AA. Inflorescence racemose, solitary or fascicled.

B. Inflorescence generally fasciculate; ocreae large and flaring, conspicuously striate. ..... *C. fallax.*

BB. Inflorescence solitary, rarely with a smaller one at the base.

C. Lianas or woody plants with scrambling branches.

D. Branches scandent or entire plant with flattened stems through bilateral cambial activity; flowers and fruit on pedicels longer than ocreolae. ..... *C. dussii.*

DD. Branches uniformly thickened; pedicels scarcely, if at all, exceeding ocreolae in flower; fruit on conspicuous pedicels.

E. Leaves of normal shoots usually oblong-elliptic, coriaceous, shining when dry, flat, coarsely and conspicuously reticulate veined, the apex rounded to emarginate; fruit large, 1.8–2 cm. long, 1–1.2 cm. thick; fruiting hypanthium rugose when dry, thick and brittle. ..... *C. ascendens.*

EE. Leaves of normal shoots not oblong-elliptic, thinner in texture, usually acute or acuminate at the apex; fruit smaller; hypanthium thin and vascular.

F. Leaves ovate, chartaceous, flat, the apex acuminate, the ultimate venation finely reticulate; stems hollow; inflorescence slender. ..... *C. striata.*

FF. Leaves ovate to obovate-oblong on normal branches, the blades usually umbonate between the veins, the apex acute; branches solid; inflorescence stout. .... *C. nitida.*

CC. Trees or shrubs, branches not noticeably scandent.

G. Pedicels conspicuously longer than the ocreolae in flower and fruit.

H. Leaves basically orbicular, as broad as or broader than long, one or both basal lobes overlapping the petiole.

I. Leaves conspicuously rugose and pubescent; fruit globose or ovoid, 0.5–0.6 cm. long. ..... *C. pubescens.*

II. Leaves conspicuously fleshy, not rugose, glabrate; fruit obpyriform, 1.2–2 cm. long. ..... *C. uvifera.*

HH. Leaves basically ovate to elliptic, longer than broad, narrowed or rounded at the base. ..... *C. diversifolia.*

GG. Pedicels shorter than or scarcely exceeding the ocreolae in flower and generally in fruit.

J. Plants deciduous; ocreae membranaceous, translucent and usually deciduous for all of its length (Trinidad species).

K. Leaves of normal shoots usually broadest above the middle, narrowed toward the base, the midrib not sharply keeled below, the blades turning black on drying. .. *C. nigrescens.*

KK. Leaves of normal shoots usually broadest below the middle, round to cordate at the base, the midrib sharply keeled, the blades at most darkening slightly on drying. ..... *C. cruegeri.*

JJ. Plants not noticeably deciduous; ocreae not membranaceous, the base at least coriaceous and persisting.

L. Achene surrounded by the perianth lobes, the ocreolar sheath commonly elongating with the pedicels, the bracts usually black. ..... *C. venosa.*

LL. Achene surrounded by the hypanthium, the perianth lobes appressed and imbricate or coronate on the achene, the bracts not conspicuously dark in color.

M. Perianth lobes appressed and imbricate in fruit, the fruit triangular in cross section; leaves ovate to suborbicular, 2–5 cm. long, cordate at the base. ..... *C. krugii.*

MM. Perianth lobes coronate in fruit (fruit not known for *C.* × *boxii*), the fruit round in section; leaves larger.

N. Leaves cordiform-ovate, broadest below the middle, 11 × 6.5 to 27 × 17.5 cm. long and broad, the base obliquely auriculate-cordate or rounded and evenly cordate. ..... *C.* × *boxii.*

NN. Leaves ovate to ovate-elliptic, smaller, generally narrowed below the middle.

O. Petioles arising above the base of the ocreae, the base of the blade auriculate at the junction with the petiole, the ultimate venation not conspicuous. ..... *C. novogranatensis.*

OO. Petioles arising from the base of the ocreae, the base of the blade slightly decurrent on the petiole, the ultimate venation reticulate and slightly elevated. ..... *C. swartzii.*

Coccoloba ascendens Duss ex Lindau, Engl. Bot. Jahrb. 13: 156. 1890.

Coccoloba ascendens Duss mss. in herb. Krug & Urban; Ann. Inst. Col. Marseille 3: 168. 1897, in part.

Coccolobis quadrifida Britton, Bull. Torrey Bot. Club 53: 467. 1926.

Coccoloba urbaniana Lindau, Engl. Bot. Jahrb. 13: 155. 1890 (as to Trinidad specimens cited but not description).

Climbing shrub or liana, much branched, the branches to 50 feet long, glabrous, occasionally hollow; ocreae membranaceous, deciduous, cut to the base, 17–20 mm. long, acuminate at the apex, glabrous to lightly puberulent; petiole inserted below the ocrea, stout to slender, 1–2.5 cm. long, flattened adaxially with a narrow compressed groove, glabrous; leaf blades elliptic, obovate, oblong, rarely ovate, 11 × 6, 13 × 8 to 17 × 14.5 cm. long and broad, coriaceous, glabrous on both surfaces, the apex rounded, acute or emarginate, the base rounded to cordate, the midrib and primary veins prominent below, distinct but not prominent above, the primary veins 5–7 pairs, arcuate anastomosing near the margin, the ultimate venation reticulate and conspicuous on both surfaces; juvenile leaves of the current year's lateral shoots elliptic-lanceolate, 14 × 7 to 20 × 8.5 cm. long and broad, the apex acute to acuminate, the base acute; leaves of adventitious shoots on petioles 3–5 cm. long, the blades ovate to elliptic-ovate, 30 × 20 to 45 × 30 cm. long and broad, the apex acute, the base rounded to slightly cordate; inflorescence axillary or terminal, 13–17 cm. long, the basal ocrea

1 cm. long, densely ferrugineous puberulent, the rachis puberulent, the bracts broadly ovate, 2 mm. long and broad; ocreolae 2 mm. long, shallowly lobed; flowering pedicels to 2 mm. long; hypanthium 1.5 mm. long, the perianth lobes 1.5–2 mm. long and broad; stamens 8, the filaments to 2 mm. long, united at the base; pistil rudimentary, to 1.5 mm. long; staminate flowers 2–3 per nodule, the pistillate flower borne singly; hypanthium and perianth similar but stamens rudimentary, functional pistil to 2 mm. long; fruiting inflorescence to 30 cm. long, the rachis to 4 mm. diameter at the base, the mature pedicels 3–4 mm. long, the fruit conspicuously articulate; fruit 1.8–2.4 cm. long and 1–1.2 cm. in diameter; fruiting hypanthium thick, slightly woody, with 11 bundles, the achene chestnut brown, smooth and shiny when dry.

LOCAL NAMES: *liana baur* (Dominica), *liane cacao* (St. Lucia), *cuchape* (Trinidad).

DISTRIBUTION: Guadeloupe to Trinidad (and possibly South America).

Guadeloupe: Ravine Chaud, *Questel 752* (US), *Duss 2180* in part (C, US); Baines Jaunes, *Stehlé 388* (US), *1036* (NY), *1501* (US), *1989* (US), *Howard 11796* (GH), *11812* (A, GH); Fonfarabre, *Stehlé 3023* (NY); without location, *Duchassaing* (B). **Dominica:** Carib reserve on Castle Bruce trail, *W.H. & B.T. Hodge 3334* (GH); Between Pointe Ronde and Milton Estate, *W.H. & B.T. Hodge 2669* (GH); Between Riverdale and Deux Branches, *Howard 11758* (GH), *11771* (GH). **Martinique:** Fonds St. Denis, Morne Rouge, *Duss 36* (B, NY, US); Morne Juin, *Hahn 1005* (B-LECTOTYPE, GH, US). **St. Lucia:** Quilesse, *P. Beard 1089* (GH, MO, S), *Howard 11676* (GH); Barre d'Isle, *Howard 11388* (GH); Castries-Dennery Rd., *Howard 11336* (GH); Patience near Micoud, *Howard 11602* (GH). **Grenada:** Grand Etang, *Howard 10660* (GH); without location, *Broadway 1206* (FM). **Trinidad:** Arima valley near Simla, *A.C. Smith 10103* (A); Aripo Savannah at Waller Field, *Howard 10316* (GH), *10341* (GH), *10452* (GH), *10507* (A); Aripo road near ¾ mile post, *Broadway 5992* (K); Blanchisseuse road N. of Arima, *Broadway 7467* (BM), *Howard 10371* (A, GH); Brazil, *Britton, Britton & Freeman 2139* (GH, K, NY); Caparo, *Broadway 2760* (FM); Cleaver wood west of Arima, *Simmonds 189* (TRIN); Cumaca road, *Simmonds 322* (TRIN); Between La Brea and Irois, *Crueger 2694* (TRIN), *2695* (TRIN), *2696* (S, TRIN); Long Stretch, 22–23-mile post, *Broadway 6942* (BM, FM, GH, K, MO, S); Maravel, collector unknown (TRIN *5953*); Mt. Tucuche, *Baker 14329* (TRIN), *14816* (TRIN), *Williams 11012* (NY–TYPE of *C. quadrifida*, TRIN); Southern Guyapo road, *Broadway 6142* (A, BM, K, S); Toco road near Sangre Grande, *Howard 10367* (GH).

Coccoloba ascendens in the Antilles is a clearly distinct species characterized by being a liana with shiny, coriaceous and heavily veined leaves and having a large fruit with a thick, vascular hypanthium. In the original description, Lindau cites material from Brazil which I have not seen and which is not represented in the material from the Berlin Herbarium. It would be unusual if this species were not found in the Guianas or Brazil; there may even be an older name for the species.

Lindau cited a number of specimens in the original description without indicating a holotype. The specimens in the Berlin Herbarium carry no

designation to indicate a type and therefore the collection *Hahn 1005* from Martinique is selected as the type collection, with the lectotype being in the Berlin Herbarium. In 1897 Duss redescribed *Coccoloba ascendens*, including with his description the citation of specimens which Lindau had previously described as *C. dussii*. It is unfortunate that one large collection, *Duss 2180*, selected by Lindau as the type of *C. dussii*, is a mixed collection and was included by Duss in his description. While the specimen of *Duss 2180* in the Berlin Herbarium represents the taxon described by Lindau as *C. dussii*, a great number of the other collections of this number represents *C. ascendens*.

In habit *Coccoloba ascendens*, as I have seen it in the field, is a scrambling shrub or a liana. The plants were generally climbing to the tops of the tallest trees. If these were small, the plants of *C. ascendens* formed a heavy tangle on and through the low shrubs. Leaf variation on a single plant was tremendous. Different types of leaves seem to be produced by the mature wood, the young shoots and the adventitious branches. The greatest variation in leaf size and type was seen in specimens in St. Lucia. I made one collection (*Howard 11336*) where trees had recently been cut along the Castries-Dennery road. The plants on the edge of this clearing had some branches sprawling out into the cleared area while other branches climbed into the undisturbed woods. On one such plant some stems were hollow while others retained the solid pith. Some stems had lanceolate-elliptic leaves, acuminate to acute at the apex and the base, while other branches of the same plant had leaves broadly ovate-oblong, acute at the apex and truncate to cordate at the base. Variation in texture was evident in the thin, young shade leaves in contrast to the larger coriaceous leaves in full exposure to the sun. Similar variation was found on plants in the forest reserve in the center of the island. A plant of a coastal river valley had thick basal stems with leaves to 45 cm. long and 30 cm. wide, while the scrambling branches produced oblong leaves averaging 13 × 9 cm. long and broad.

Coccoloba quadrifida described by Britton is clearly a restricted growth form of *C. ascendens*. Britton reports his plant to be a small tree instead of the usually liana type, but the cited material, as well as subsequent collections from the same area, show clearly the variation that makes *C. quadrifida* the same as *C. ascendens*.

Many of the specimens cited above bear an unpublished specific name referring to the island of Guadeloupe. These are not distinguishable from *C. ascendens* in other parts of its range.

Coccoloba urbaniana was described by Lindau in his monograph of the genus in 1890. He cited specimens from Trinidad (*Crueger 2694, 2696*) and from Puerto Rico (*Sintenis 1527, 1585*); however, the description published fits only the Puerto Rican material. In a subsequent treatment of the West Indian species (Symb. Ant. 1: 225. 1899), Lindau again cites the Puerto Rican specimens but fails to list the Crueger specimens anywhere in the treatment. Britton later redescribed the Puerto Rican material as *C. borinquensis*, stating that Lindau had erroneously included this

in *C. urbaniana* of Trinidad. As no type was selected for *C. urbaniana* and the original author chose to limit the species to Puerto Rico, I feel that the species name has no validity in the Trinidad flora. *Coccoloba urbaniana* is best considered as a form of *C. swartzii* (Jour. Arnold Arb. 37: 328. 1956).

A most striking variation was found in the plants of this species growing in the Aripo Savannah. A number of specimens were found with the staminate and pistillate flowers on different branches of the same plant. Most of the species of *Coccoloba* which I have studied in the field have been completely or functionally dioecious. This was also true of the majority of plants found in the savannah area. However, there were enough monoecious plants seen in this area to suggest the need for careful field study in the South American species of this genus.

One collection seen but not cited above is *Duss 72*, represented by one specimen in the New York Botanical Garden herbarium. The handwritten label reports the plant to be from Antigua. During my visit to Antigua I failed to find a single ecological location which might possibly have supported the species. Since other recent collectors have not reported the species, I suspect that the label of this specimen is in error.

Coccoloba × boxii Sandwith (pro sp.); Howard, Jour. Arnold Arb. 37: 329. 1956.

Coccolobis boxii Sandwith, Jour. Bot. 78: 97–98. 1940.

Tree to 8 m. tall; current year's branches cinereous, striate, sulcate, pubescent; ocreae to 1.5 cm. long, densely pubescent, the base persistent, sub-coriaceous, the apex membranaceous-evanescent; leaves cordiform-ovate, 11 × 6.5 cm. long, 27 × 17.5 cm. broad, coriaceous, light, midrib pubescent; lateral veins 8–12, slightly prominent; petiole densely pubescent, 0.7–1.3 cm. long; apex obtuse, the base oblique, auriculate-cordate or rounded to nearly evenly cordate; inflorescence solitary, simple, 17–22 cm. long; rachis 1.5–2 mm. wide, sulcate, densely minutely pubescent, the nodules 1–4-flowered, the bracts broadly triangular-ovate, rounded-obtuse, 1.3 mm. long, 2 mm. wide, conspicuously pubescent, the ocreolae 2 mm. long, membranaceous, flaring, almost bilobed, glabrous at the base; pedicels to 0.75 mm. long, the hypanthium 1.3 mm. long, the perianth lobes ovate-obtuse, 2 mm. long, 1.75 mm. broad, the interior smaller, the filaments (in bud) 0.6 mm. long; ovary ovoid-ellipsoidal 2.3 mm. long, 1.3 mm. in diameter, glabrous; styles shorter than the ovary, about 0.75 mm. long.

Antigua: Pelican Bay, *Box 539* (BM, US), *1497* (BM-HOLOTYPE, US).

The suggested hybrid nature of this species and the possible parents, *C. uvifera* and *C. swartzii* or *C. swartzii* forma *pubescens*, have been discussed in a previous paper.

Coccoloba cruegeri Lindau, Engl. Bot. Jahrb. 13: 209. 1890.

Coccoloba ernstii Johnston, Proc. Amer. Acad. 40: 685. 1905.

Tree to 12 m. tall, d.b.h. 30 cm., the wood extremely hard and tough,

the bark gray; young stems glabrous, ash-colored, striate, solid; ocreae 4–5 cm. long, membranaceous and translucent when dry, deeply split, deciduous; leaves deciduous, the petioles 2–3 cm. long, deeply grooved above, glabrous, inserted at the base of the ocrea, the blades ovate-elliptic to suborbicular, 14 × 12 to 22 × 16 cm. long and broad, coriaceous when mature, glabrous, the apex acute to rounded, the base rounded, the margin flat, the midrib prominent above, sharply keeled below, the primary veins 6–8 pairs, slightly prominent above, sharply keeled and prominent below, slightly decurrent on the midrib, straight becoming arcuate and anastomosing near the margin, the secondary veins and nerves reticulate; leaves of adventitious shoots with ocreae to 7 cm. long, on petioles 5 cm. long, blades mostly elliptical to 54 cm. long and 32 cm. broad, with 11 pairs of conspicuous primary veins; inflorescence racemose, laxly flowered, 7 cm. long, the rachis angled when dry, puberulent, the bracts ovate, 0.5 mm. long, the ocreolae membranaceous 0.75 mm. long, the pedicels tenuous, as long as the ocreolae, the hypanthium glabrous, 1 mm. long, the perianth lobes ovate to oblong, 1 mm. long, only staminate flowers known, these borne singly with functional stamens exserted on filaments 1.25 mm. long, the pistil rudimentary; immature fruit (according to Lindau) subglobose, the lobes of the fruiting perianth conspicuous to the base.

DISTRIBUTION: Trinidad and Margarita.

Trinidad: Without specific location, *Crueger 113* [TRIN *778*] (GOET-TYPE, NY, TRIN); Monos Island, *Howard 10415* (GH); Aripo Savannah, *Howard 10505* (GH); Toco Road between Arima and Sangre Grande, *Howard 10365* (GH).

Lindau assigned *Coccoloba cruegeri* to his section Campderia, believing that the perianth lobes surrounding the achene remained free in fruit. The associated characters of this section of black-colored bracts and normally large, conspicuous ocreolae were not described by him and cannot be seen on the type material. The specimens in Berlin and Goettingen do not have fruits, in spite of Lindau's description of them, and the material in the Trinidad Herbarium has only fragments of a flowering inflorescence axis. Therefore it seems unwise to assign *C. cruegeri* to the section Campderia.

Lindau cites specimens for this species as "*Crueger 113, 778*" (Engl. Bot. Jahrb. 13: 210. 1890). Examination of the original material which is preserved in the Trinidad Herbarium shows that Crueger assigned his own collection numbers to some specimens and failed to do so to others. However, nearly all sheets were assigned numbers for the Trinidad Herbarium and in the present case the "113" is Crueger's number while the "778" is the serial number of the collection in the Trinidad Herbarium. The original collection of this material was assigned by Grisebach to *Coccoloba plumieri*, according to the label on the specimen, although this information was never published. The label also indicates that the collection was made in the vicinity of Caroni.

There is a strong similarity between *Coccoloba nigrescens* and *C. cruegeri*, and perhaps future collections of more adequate material will indicate either that they are the same or that material called *C. cruegeri* is in reality

a hybrid population. Both species are unique in the Trinidad area in having deciduous leaves. *Coccoloba nigrescens* appears to develop flowers when the leaves are very small, while *C. cruegeri* has nearly mature leaves before any indication of the inflorescence is produced. I found only one plant in flowering condition and on this the flowers were just beginning to open. These were borne singly at the nodules and were staminate.

The several plants seen in the field all possessed multiple trunks but were without indication of injury. One trunk possessed leaves much larger than normal as described above. In both normal and adventitious shoots the leaves were characterized by the remarkably sharply keeled midribs. In this characteristic the plant could be distinguished easily from neighboring plants of *C. nigrescens*. Several of the local residents were familiar with plants assigned to these two species. They recognized these as "grapes" similar to *Coccoloba uvifera* but could not recall having seen fruits on the trees.

Coccoloba ernstii Johnston described from Margarita Island is to be referred here. The type specimen (*Johnston 250*) in the Gray Herbarium indicates that this tree, also, is deciduous and that the young leaves and inflorescences are comparable to the material cited from Monos. Johnston indicated the alliance to *C. cruegeri* in his original description.

Coccoloba diversifolia Jacq. Enum. Pl. 19. 1760, Hist. Stirp. Amer. 114. *pl. 76*. 1763.

Coccoloba cubensis Meisner, DC. Prodr. **14**: 162. 1857.

Coccoloba laurifolia Lindau, Engl. Bot. Jahrb. **13**: 158. 1891, and all recent authors, not Jacquin.

Coccoloba longifolia Schmidt, Rep. Spec. Nov. **24**: 73. 1927, not Fischer ex Lind.

Shrub or tree to 8 m. tall; branches terete, often geniculate by limited growth, glabrous, the nodes rarely slightly swollen; ocreae coriaceous in the persistent lower portion, membranaceous and deciduous above, 3–5 mm. long; leaves of normal shoots with petioles 7–10 mm. long, glabrous, arising from the base of the ocreae; blades ovate, oval, oblong, elliptic, lanceolate or obovate, variable on one branch, 4 × 3.5, 7 × 5.5, 8 × 4.5, 12 × 8 cm. long and broad, coriaceous, often shining above, dull beneath, glabrous, the apex rounded, obtuse, acute or acuminate, the base cuneate, rounded or subcordate, the margin entire; midrib and primary veins slightly prominent above, the secondary venation reticulate on both surfaces, the primary veins 3–7 pairs, arcuate, anastomosing before reaching the margin; leaves of adventitious shoots on petioles 1–2.5 cm. long, with blades of varying shapes 17 × 8, 24 × 13, to 32 × 12.5 cm. long and broad; leaves of windswept specimens often much smaller than those of normal shoots with blades 2 × 1.3 to 3 × 2 cm. long and broad; inflorescence terminal 4.5–18 cm. long, the rachis glabrous, the flowers on pedicels 2–4 mm. long, the staminate flowers 2–4 at each locus, the pistillate flowers borne singly at each locus, the bracts ovate, less than 0.5 mm. long, the ocreolae membranaceous, less than 0.5 mm. long, the hypanthium 1 mm. long, the

perianth lobes ovate to oblong, 2–3 mm. long, 1–2 mm. broad, the functional stamens 1 mm. long, the sterile stamens rudimentary; fruiting pedicels 3–4.5 mm. long, the fruit globose to obpyriform, 10 × 7, 12 × 8, 13 × 8 mm. long and in diameter, the apex rounded, the perianth lobes imbricate and appressed.

DISTRIBUTION: Florida, the Bahamas, the Greater Antilles and Antigua.

Antigua: Pelican Bay, *Howard 11990* (GH).

Coccoloba dussii Lindau, Notizblatt Berlin 1: 213. 1896, Symb. Antil. 1: 226. 1899; Duss, Ann. Inst. Col. Marseille 3: 167. 1897.

Coccoloba scandens Benth. in obs. Lond. Jour. Bot. 4: 625. 1845, nomen.
Coccoloba excelsa Smith (?), Kew Bull. 1893: 272. 1893.

Woody shrub with scrambling branches or a vine; young stems terete, minutely short pilose becoming glabrous, the older stems flattened through bilateral development; ocreae to 1 cm. long, membranaceous, deciduous; petiole inserted below the ocrea, 2.5–4 cm. long, minutely pilose; blades ovate to oblong, 6.5 × 4.5, 12 × 7.5 to 17 × 10.5 cm. long and broad, thin-coriaceous, glabrous, the apex acute to short-acuminate, the base rounded to slightly cordate, the margin entire, the midrib prominent below, slightly keeled above, the secondary veins 7–8 pairs, arcuate, anastomosing near the margin, the ultimate venation reticulate and conspicuous on both surfaces; leaves of adventitious shoots on petioles 3.5 cm. long, the blades broadly ovate to elliptic-ovate, 25 × 16 to 30 × 19 cm. long and broad, the apex rounded to acute, the base broadly cordate; leaves of younger shoots elliptic-lanceolate, 19 × 10 to 24 × 10.5 cm. long and broad, the apex acuminate, the base rounded or acute; inflorescence terminal, 9–15 cm. long, the basal ocrea 1.3–4.3 cm. long, the rachis minutely pilose or puberulent, the bracts less than 1 mm. long, the ocreolae 0.5 mm. long, the flowering pedicels to 3 mm. long, the hypanthium 2 mm. long, the perianth lobes ovate, 2 mm. long, the staminate flowers borne 2 or 3 at a node, the pistillate flowers not known; fruiting pedicels 4–6 mm. long, usually slightly reflexed, slender, the mature fruit short stipitate, spherical, dark blue-purple in color, extremely astringent, the surface of dried fruit rugose, the fruiting perianth tightly adherent to the achene, the achene dull brown, rugose.

LOCAL NAMES: *Raisinier marron, Raisin marron* (Guadeloupe).

DISTRIBUTION: Guadeloupe, St. Lucia, St. Vincent, Grenada, Trinidad and Tobago.

Guadeloupe: Ravine Chaude (Lamentin), *Duss 2180* (B–TYPE, C, FM, NY); Between Pointe Noire and Ravine Chaude, *Duss 3711* (B, FM, NY, US); Between Lamentin and Pris d'Eau, *Howard 11852* (A, GH); Grande Savane, Gourbeyre, *Duss 3430* (B, NY); Goyave, Pont Moreaux, *Stehlé 931* (US); Basse Terre near Duclos, Petit Bourg, *A.C. Smith 10347* (A). **St. Lucia:** Without location, *Anderson s.n.* (K). **St. Vincent:** Silver Spoon district above Three Rivers, *Howard 11161* (GH), *11185* (GH), *11189* (GH). **Grenada:** Grand Etang, *Howard 10656*

(GH). **Tobago:** Easterfield, *Broadway 4371* (NY); The Widow, *Broadway 4653* (K, MO). **Trinidad:** Between Arima and Sangre Grande, *Howard 10362* (GH); Blanchisseuse Road, *Broadway 6456* (A); Morne Bleu, *Britton, Freeman & Bailey 2271* (GH).

Similar to many other lianas, *Coccoloba dussii* varies according to the attitude of the stem and its branches. Over fifty feet of liana was pulled from trees or untangled from prostrate growth in several locations to determine the range of leaf variation in single plants. Basal leaves which persisted on the older stems were usually larger than the others on the plant. Leaves on apical portions of the stem were usually longer and narrower than the other leaves, while the smallest leaves occurred on the lateral flowering or fruiting branches. Such flowering branches are represented by most of the herbarium specimens cited. Flowering branches which were twisted around limbs of the supporting trees as an aid in climbing had the smallest leaves and the shortest inflorescences.

The bilateral development of the older stems was conspicuous. Such stems were often 5–6 times as wide as thick. Young stems were cylindrical but slightly fluted, with a conspicuously large pith.

Coccoloba dussii is similar to *C. excelsa* and in sterile condition it is often difficult to distinguish between them. In most South American material of *C. excelsa* the leaves, young stems and inflorescences are conspicuously pubescent. In some South American material the pubescence has been lost, leaving relatively large hair bases with evidence of hairs only along the midrib, on the lower surface of the lamina and in the axils of the lateral veins. Such hair bases have often been mistaken for glands or secretions. Both functionally staminate and pistillate flowers of *C. excelsa* are known and in each the ocreolae surrounding the flowering pedicels are large, membranaceous and more or less persistent, almost equalling the pedicels in length in flowering condition. Only staminate flowers are known for *Coccoloba dussii* and in these the ocreolae are small and less than 1/5 the length of the pedicels. The inflorescence rachis and the ocreolae are only slightly puberulent. I have not observed *C. excelsa* in the field, but on the basis of herbarium material alone the character of the ocreolae in flowering condition is sufficient to distinguish the species. The fruits likewise are similar, as is the growth habit, and the appearance of the leaves in dried condition. In general the leaves of *C. dussii* tend to be more umbonate between the veins and to have thinner and slightly longer petioles. The flowers are commonly reflexed on the inflorescence, although this characteristic may be associated with the growth habit of the plant. Further field study and additional collections may indicate that *C. dussii* should be considered a variety of, or even synonymous with, *C. excelsa*.

Lindau described *Coccoloba dussii* in 1896, citing only one specimen, *Duss 2180*, in the herbarium of Krug and Urban. The type in the Berlin Herbarium consists of one branch and is as Lindau described. Other specimens bearing this collection number are mixtures of *C. dussii* and *C. ascendens*.

In describing *Coccoloba excelsa*, Bentham notes that "In Forsyth's

herbarium, I found, under the name of *C. scandens*, an imperfect specimen of a plant gathered by Anderson in Saint Lucia, very much like the above, but with the leaves perfectly smooth, the racemes much longer and the bracts very small. These are the only two species as yet known to be climbers." I have seen the plant from Bentham's herbarium which is now in the collection at the Royal Botanic Garden at Kew. It is a fragment consisting of two leaves and one inflorescence; the latter is staminate, but very few flowers remain. The specimen is better referred to *C. dussii* than to *C. excelsa*. It is to be expected that more thorough exploration of St. Lucia will reveal *C. dussii*, which has not been reported in recent collections from that island. *Coccoloba dussii* is known from Guadeloupe, but has not been found on Martinique or Dominica to the present.

Coccoloba fallax Lindau, Engl. Bot. Jahrb. 13: 172. 1890.

Coccoloba crescentiifolia Griseb. Fl. Br. W. I. 163. 1859, not Cham.

Tree to 10 m. tall (Swabey), d.b.h. 6 cm.; branches thick, strongly striate; ocreae coriaceous, 2–4 cm. long, flaring, strongly bilobed, conspicuously striate, glabrous; petioles arising from the base of the ocreae, 2.5–4.5 cm. long, stout, deeply grooved, striate, glabrous; leaf blades oblong-ovate to oblong-obovate, 14 × 5, 23 × 10, 25 × 11, 36 × 13 cm. long and broad, thick-coriaceous, glabrous, the apex acute to acuminate, the base rounded or narrowed, the ultimate base slightly cordate, the midrib conspicuous above, keeled, sulcate or grooved at both sides, strongly keeled and conspicuous below, the veins 7–10 pairs, ascending arcuate, anastomosing near the margin, slightly impressed above, conspicuous below, the ultimate venation reticulate but inconspicuous; inflorescence lateral, fasciculate, racemose, laxly flowered, the basal ocreae conspicuous, coriaceous 3 cm. long, mostly persisting, commonly strongly keeled or striate, glabrous or puberulent, the rachises 7–23 cm. long, puberulent, the flowers borne singly at each nodule, the bracts ovate, minute to 0.5 mm. long, puberulent, the ocreolae puberulent, scarcely exceeding the bracts, the staminate flowers with pedicels 2–3 mm. long, puberulent, the hypanthium 1 mm. long, the perianth ovate, the lobes 1.5 mm. long, the functional stamens with filaments 2–2.5 mm. long, the pistillate flowers not seen; fruiting pedicels 2–3 mm. long.

LOCAL NAMES: *Black grape* (Trinidad).

DISTRIBUTION: Trinidad and Venezuela.

Trinidad: Without locality, *Crueger 114* (GOET-TYPE), *779* (TRIN); S. W. Reserve, *Swabey* [TRIN 12292] (NY); Cat's Hill Reserve, *Swabey* [TRIN 12543, 12536]; Black River, *Freeman 8102* (NY, TRIN); Windbelt Reserve, *Brooks* [TRIN 12502] (NY). **Chacachacare:** *Britton, Freeman & Watts 2694* (GH, NY, TRIN). **Venezuela:** Cristobal Colon, *Broadway 685* (GH); Cariaquita, *Bond, Gillin & Brown 244* (GH); Fundo la Argentina, *Delgado 209* (A).

Coccoloba fallax is very similar to *C. densifrons* and *C. padiformis*. When more adequate material is available, especially when there is a good

series of fruits and more information on the growth habits, these species may be considered to be merely varieties, or even identical.

I was unable to find *Coccoloba fallax* in Trinidad or on Chacachacare. Data on the specimens cited are inadequate for a complete understanding of the form of the plants. No female flowers are known and the few fruits associated with specimens collected by Swabey (TRIN 12536) and Freeman (TRIN 8102) are crushed and in poor condition. The fruits were probably round or spherical with imbricated perianth lobes. The achenes were a pale tan color in the material seen, apparently also spherical and very thin-walled.

Swabey reports that one specimen which he collected grew as a clump tree of 2 to 6 stems. Some of these reached 30 feet in height. Neither these nor other specimens studied appeared to represent adventitious shoot material.

At present *Coccoloba fallax* seems distinct on the basis of the fascicled inflorescence of simple racemes, the conspicuously large ocreae, particularly those of the inflorescence, and the strongly keeled midribs of the leaves.

Coccoloba krugii Lindau, Engl. Bot. Jahrb. **13**: 145. 1890; Symb. Antil. **1**: 222. 1899; Howard, Jour. Arnold Arb. **37**: 337. 1956.

Coccoloba børgesenii Schmidt, Rep. Spec. Nov. **24**: 75. 1927.

Coccoloba børgesenii forma *ovato-lanceolata Schmidt*, Rep. Spec. Nov. **24**: 76. 1927.

Shrub or small tree to 6 m. tall; branches terete, glabrous, slightly geniculate and nodose; ocreae membranaceous, persistent, 3–5 mm. long; leaves of normal shoots with petioles 5–6 mm. long, corky at the base, arising from the base of the ocreae; blades ovate to suborbicular, 2 × 1.8, 4 × 3.5, 5 × 4 cm. long and broad, thin-coriaceous, glabrous or rarely with a few hairs near the attachment of the petiole, the apex obtuse or rounded, the base cordate or rounded, the margin flat or recurved; midrib flat above, slightly prominent below, the primary veins 4–6 pairs, straight bifurcating and anastomosing near the margin, flat on both surfaces, the secondary venation minutely reticulate below, smooth above; leaves of adventitious shoots with petioles 1 cm. long, the blades cordate or elliptic to 7 × 6 cm. long and broad; inflorescence terminal 5–8 cm. long, the rachis glabrous, the staminate flowers 1–3 per node, the pistillate flowers borne singly, the bracts broadly ovate, membranaceous, 1 mm. long; ocreolae membranaceous, flaring to 1 mm. long; pedicels wanting or shorter than the ocreolae, the hypanthium 1 mm. long, the perianth lobes ovate, to 2 mm. long, the filaments of fertile stamens 1.5 mm. long; fruit ovoid or angularly fusiform, strongly triangular in outline, 4–5 mm. long, 3–3.5 mm. in diameter, the perianth lobes appressed, about half the length of the fruit.

DISTRIBUTION: The Bahamas, Hispaniola, Jamaica, Puerto Rico, the Virgin and the Leeward Islands.

Antigua: Goble creek near Gaynors, *Box 1388* (A, GH, US).

Coccoloba latifolia Lam. Encycl. 6: 61. *t. 316, f. 4.* 1804; Lindau, Engl. Bot. Jahrb. 13: 133. 1890.

Small tree to 15 m. tall, d.b.h. to 45 cm.; branches thick, angular and vertically ridged at least when dry, hollow but septate at the nodes, glabrous; ocreae large, conspicuous, coriaceous, tubular or sub-campanulate, 3–7 cm. long, glabrous, acute to strongly bilobed; leaves of flowering branches variable in size, the petioles generally 2–3 cm. long, glabrous or puberulent or occasionally with long pilose hairs; blades generally orbicular to obovate, 13 × 10, 20 × 15 to 28 × 28 cm. long and broad, coriaceous, glabrous or with scattered pilose hairs on the midrib and veins on the lower surface, the apex rounded or emarginate to short acuminate, the base rounded to deeply cordate, the margin flat or strongly recurved, entire, often undulate; midrib and veins impressed above, conspicuous below, the primary veins 9–12 pairs, arcuate and anastomosing near the margin, the secondary venation conspicuous, the blade strongly bullate between the primary veins or between the secondary veins as well as the primary or scarcely bullate and nearly flat; leaves of adventitious shoots larger with petioles to 5 cm. long and blades to 48 × 50 cm. long and broad or larger, similar in other characteristics; inflorescence terminal, panicled to 30 cm. long and broad, with solitary or 2–3-fascicled undivided pseudoracemose branches or rarely the lowest branch paniculate, the rachis puberulent, the staminate flowers 1–3 per node, the pistillate flowers usually borne singly but some apparently 3–4 per node, the bracts minute, to 0.5 mm. long, the ocreolae membranaceous to 0.75 mm. long, the pedicels very thin 1–2 mm. long, the hypanthium tapered at the base, 1–1.6 mm. long, the perianth lobes 1.5 mm. long, the functional stamens with filaments to 2 mm. long; fruit ovoid, 7–10 mm. long, 5–6 mm. in diameter, the base rounded to slightly attenuate, the apex rounded with imbricate perianth lobes, the immature fruits showing 9 conspicuous basal nerves when dry, the mature fruit black, fleshy when fresh, the outer pericarp commonly loose, the achene dark brown shining, smooth.

LOCAL NAMES: *Grape, cuchape, stave wood, big leaf.*

DISTRIBUTION: Trinidad, Tobago, Venezuela, British Guiana, Brazil.

Trinidad: San Fernando, La Retraite, *Crueger 2690* (B, TRIN); Tamana, *Marshall* [TRIN 12313] (NY); St. Joseph, *Dannouse, s.n.* (TRIN); Aripo Savanna, *Britton, Broadway & Hazen 316* (GH, NY), *Howard 10355* (GH); Talparo, *Simmonds* [TRIN 14652]; Arima, *Eggers 1377* (C); Piarco Savanna, *Britton, Britton & Hazen 113* (NY); Chancellor Road, St. Ann's, *Broadway 8989* (TRIN); Caroni, *Eggers 912* (M); cultivated, *Broadway 4332* (TRIN). **Monos Island:** *Howard 10416* (GH).

A well-defined and easily recognized species. The trees are common in savanna areas and probably for these reasons have not been collected and so the species is poorly represented in herbaria. The wood tends to be soft and the branches are relatively brittle and fragile. An equal hazard to the collector is the occurrence of colonies of stinging and biting ants in the hollow pith and in the ocreal sheath.

Coccoloba nigrescens Lindau, Engl. Bot. Jahrb. 13: 192. 1890.

Tree to 10 m. tall; youngest stems pubescent with long strigose hairs, becoming glabrate; ocreae lax, membranaceous to extremely thin and translucent even when fresh, to 3.5 cm. long, divided 2/3 its length, acute at the apex, pubescent with long scattered hairs, deciduous to the base; petioles attached at the base of the ocreae, stout, 5–7 mm. long, densely pubescent on the adaxial surface when young, becoming glabrate; leaf blades obovate-oblong to ovate-oblong, 12 × 7 to 16 × 9 cm. long and broad, thin-coriaceous when mature, glabrous, the apex acute to rounded, rarely short-acuminate, the base cuneate or rounded, the margin slightly recurved, the midrib prominent on both surfaces, not keeled, the primary veins 6–9, mostly straight becoming arcuate and anastomosing near the margin, the lesser nerves inconspicuous; inflorescence terminal or lateral, to 10 cm. long, the peduncle 6 mm. long, strigose pubescent becoming glabrous, the bracts triangular, acute, puberulent, 0.75 mm. long, the ocreolae erect, truncate, not exceeding the bracts; staminate flowers 2 (rarely 1) per nodule, the pedicels shorter than the ocreolae, the hypanthium 0.75 mm. long, the perianth lobes ovate to 0.75 mm. long, the stamens exserted on filaments 1 mm. long; pistil rudimentary, the pistillate flowers not known; old fruiting inflorescence with stout pedicels to 1 mm. long; fruit not known.

DISTRIBUTION: Islands near Trinidad.

Chacachacare Island: *Crueger 116* (B, GOET-TYPE, TRIN), *Howard 10440* (GH). **Monos Island:** *Crueger* [TRIN 3244], *Britton & Hazen 1742* (FM, GH, NY, TRIN), *Broadway 7457* (TRIN), *Howard 10422* (GH).

Coccoloba nigrescens is apparently one of the few species of the genus which loses all of its leaves at certain seasons. However, there is no indication of this characteristic in the shape or texture of the mature leaf. Lindau described the species from specimens collected in May while the leaves and inflorescences of the plant were very young and immature. Subsequently, Britton and Hazen collected the species again on an adjacent island in the month of April and obtained specimens comparable in quality. Lindau commented on the fragility of the leaves which turn black in drying. The Broadway collection cited above was collected in November and consists of mature leaves from a sterile shrub. The collections which I made were obtained in the month of February in the type locality and in the same area where Britton visited. These also possess fully mature leaves. The leaves turn dark on drying and all parts of the plant are glabrous, lacking the hairs apparently characteristic of the younger parts. My companion in the field, a local resident and employee at the leper colony, assured me that this plant does indeed lose its leaves. At present this species is poorly represented and not well known. Further collections are needed, especially to determine whether this species is truly distinct from *C. cruegeri*. At present *C. cruegeri* may be distinguished in the juvenile leaf condition by the lack of the strigose pubescence and in mature leaf form by

the longer petioles, larger adventitious shoot leaves and the sharply keeled midrib.

Both of the Crueger specimens which represent the type collection are in very poor condition.

Coccoloba nitida HBK. Nov. Gen. **2**: 176. 1818.

Polygonum arborescens Vell. Flor. Flum. 163. 1825, **4**: *pl. 43.* 1827.
Coccoloba marginata Hooker, Jour. Bot. **4**: 626. 1845.
Coccoloba guianensis Meisner, Linnaea **21**: 264. 1848.
Coccoloba martii Meisner, Fl. Bras. **5**: 37. 1855.
Coccoloba martii Meisner var. *major* Meisner, Fl. Bras. **5**: 38. 1855.
Coccoloba nitida HBK. var. *rotundata* Meisner, Fl. Bras. **5**: 88. 1855.
Coccoloba nitida HBK. var. *cordata* Meisner, Fl. Bras. **5**: 38. 1855.
Coccoloba trinitatis Lindau, Engl. Bot. Jahrb. **13**: 182. 1890.

Plants of variable habits most commonly tree-like at the base with scrambling, liana-like branches, the nodes extremely long and the leaves much reduced at the ends of these or liana-like from the base, rarely shrub-like; branchlets terete, smooth or striate, minutely puberulent, the lenticels elliptical, conspicuous, whitish; ocreae obliquely truncate, 1–1.5 cm. long on normal as well as scrambling shoots, ferrugineous puberulent when young becoming glabrate, the base coriaceous and persistent usually tightly investing the stem; petioles inserted at the base of the ocreae, usually 1.5–2 cm. long, minutely puberulent, canaliculate above, striate; leaf blades of flowering branches ovate, elliptic, oval-oblong or obovate-oblong, 10 × 5, 13 × 6 to 20 × 8 cm. long and broad, coriaceous, shining or dull, usually drying darker above than below, glabrous on both surfaces, the apex acute, rarely acuminate or almost rounded, the base rounded to cordate, the margin flat rarely slightly recurved, the midrib and veins slightly impressed above, conspicuous below, the primary veins 8–10 pairs, arcuate, anastomosing near the margin, the ultimate venation finely reticulate; leaves of conspicuously scrambling shoots either much smaller or even larger (to 24 × 10 cm.) than those of normal flowering branches, generally of shinier texture; leaves of adventitious shoots on petioles 1.2–3.5 cm. long, with blades generally oblong or elliptic-oblong, 17 × 10 to 21 × 12 cm. long and broad, the apex usually rounded, the blade often strikingly umbonate between the primary veins; inflorescence generally terminal but often lateral, a solitary raceme, 7, 10, 22 to 36 cm. long, occasionally fascicled with one or two small racemes at the base or with 1 or 2 basal racemes developing from the main axis; rachis puberulent; bracts ovate 0.5–1 mm. long, the ocreolae strongly bilobed, membranaceous, puberulent, 1.5–2 mm. long, the staminate flowers 2 or 3 at each node, on pedicels shorter than the ocreolae, the hypanthium conical 1–1.5 mm. long, the perianth lobes ovate, 1–1.5 mm. long, the stamens 1.5–2 mm. long, the pistil abortive; pistillate flowers borne singly on pedicels about equalling the ocreolae, the stamens rudimentary and shorter than the perianth lobes, the pistil exserted, the fruiting pedicels 2–2.5 mm. long; fruit ovoid (usually 12 mm. long, 9 mm. diameter), the perianth lobes

slightly coronate, the hypanthium in fruit smooth to strongly striate when dry, the achene dark brown, smooth.

LOCAL NAMES: *Black grape* (Trinidad), *masari* (British Guiana), *pipoca* (Brazil).

DISTRIBUTION: Trinidad, the Guianas, Brazil.

Trinidad: Arima, *Howard 10359* (GH), *10368* (GH), *10506* (GH); Aripo Savannah, *Crueger 2693* (B-TYPE of *C. trinitatis*, TRIN), *Howard 10507* (GH), *Britton, Britton & Hazen 272* (GH, NY), *Baker s.n.* (HT *15122*), *Broadway* (TRIN 10480); Caroni, *Crueger 671* (TRIN); Long Stretch, *Simmonds 329* (TRIN 14255), *s.n.* (TRIN 15378); Santa Cruz, *Dannouse s.n.* (NY, TRIN); Valencia, *Broadway 5584* (A, BM, MO, S), *6652* (A, B), *8988* (TRIN), *Britton, Britton & Hazen 1023* (GH, NY); *Britton & Britton 2103* (GH, NY); without locality, *Fendler 1010* (BM). **British Guiana:** Amakura River, *De La Cruz 3552* (GH); Assakatta, *De La Cruz 4270* (GH); Barima River, *De La Cruz 3363* (GH); Bartica River, *De La Cruz 1962* (GH); Kaieteur Plateau, *Maguire & Fanshawe 23316* (A); Kuyuwini River, *Smith 3030* (A); Mazaruni Station, *For. Dept. Brit. Guiana 4269* (NY); Upper Rupununi River, *De La Cruz 1442* (GH). **Dutch Guiana:** without location, *Samuels 419* (GH), *Wullschlagel 882* (B). **French Guiana:** Acaronany, *Sagot 887* (NY); Paramaribo, *Regel 492* (NY); without location, *Broadway 307* (GH), *Leblond s.n.* (B), *Jelski* (B), *Perrottet 84* (NY), *Poiteau* (B). **Brazil:** Maranhão, Island of São Luiz, *Froes 11698* (A), *11716* (A); Minas Geraës, river San Francisco near Salgado, *Martius* (M-TYPE of *C. martii*); Bahia, Joazeiro, *Martius* (M-TYPE of *C. nitida*).

In the field there is considerable variation among plants of this species. I was fortunate to have one full week in the Arima area of Trinidad, where attention was given to the growth habits and the variation seen in plants then referred to *Coccoloba trinitatis* Lindau. The three collections made at that time (*Howard 10359, 10368 and 10506*), comprise the equivalent of 47 herbarium sheets. However, each number was made from only one plant and each number was collected on a separate wooded island in the Aripo Savannah. By carefully following the branches of each tree I was able to determine that a tenuous "liana" of one part of the forest canopy was actually the same individual as the "different" plants of the forest floor which were, in reality, either flowering branches or adventitious shoots.

As a result of this experience in the field, it seems clear to me that the specimens Lindau saw and referred to *Coccoloba nitida*, *C. guianensis*, *C. marginata* and *C. trinitatis* could all have come from one plant. They obviously did not come from one plant, but nevertheless I conclude that they represent only one species. Many of the morphological differences by which Lindau distinguished species can be found on a single plant in the field. Moreover, he failed to understand the sexual differences between staminate and pistillate plants. Meisner, Lindau's predecessor, treated as varieties the different leaf sizes on a series of specimens. These varieties "major" and "minor" are easily found on one branch in the living plant.

Coccoloba nitida will be recognized in future collections as a liana, for the flowering branches are usually short lateral shoots on a scrambling branch system. The flowers are a clearer white than most of the *Coccoloba*

species I have seen in the field and the staminate inflorescence in full flower is conspicuous. The long inflorescence, the membranaceous, bilobed ocreolae and the ovate fruits aid in the determination of this species.

Coccoloba novogranatensis Lindau, Engl. Bot. Jahrb. 13: 192. 1890.

Coccoloba caribaea Urban, Symb. Antil. **5**: 337. 1907.

Shrub 2 m. to tree 27 m., trunk commonly muscular, the bark red; branchlets terete, glabrous, the nodes slightly swollen; ocreae cylindrical, the upper portion membranaceous and deciduous, the lower portion coriaceous and persistent; leaves of normal shoots with petioles 8–11 mm. long, puberulent when young, with age glabrous except in the groove, attached above the base of the ocreae; blades ovate to ovate-elliptic, 6 × 4, 9 × 5, 10.5 × 5.5 cm. long and broad, thin-coriaceous, glabrous above, glabrate below except for long hairs along the midrib at the base of the blade, the apex attenuate, the base narrowly cordate, the margin entire; midrib and primary veins inconspicuous above, prominent below, the primary veins 5 or 6 pairs, the ultimate venation finely reticulate; leaves of adventitious shoots generally similar but occasionally obovate and narrowed at the base, ovate-lanceolate or lanceolate-elliptic, the blades 11 × 7 to 18 × 15 cm. long and broad, the basal lobes of leaves on adventitious shoots often overlapping; inflorescence terminal on short lateral shoots, 3–9 cm. long, the basal ocreae 5–10 mm. long, bilobed at the apex, the rachis glabrous, the flowers commonly borne singly at each nodule (occasionally 2 in staminate plants), the bracts oblong; 2 mm. long, 0.5–0.75 mm. broad, the ocreolae 3 mm. long, bilobed at the apex, membranaceous and persistent, the pedicels 2.5–4 mm. long, the hypanthium 0.75 mm. long, the perianth lobes ovate, 1.5 mm. long and broad, the functional stamens 2.5 mm. long, the functional pistil 2 mm. long; fruit generally spherical with coronate perianth lobes, occasionally narrowed at the base, 1 cm. long, 5–9 mm. in diameter, the achene brown, shining.

Distribution: St. Vincent, Grenada, Trinidad, Tobago, Margarita, Colombia, Venezuela and Panama.

St. Vincent: *H.H. & G.W. Smith 1790* (B, NY). **Grenadines:** Bequia, *Howard 11231* (GH), *11241* (GH); Cannuoan, *Howard 11091* (GH); Carriacou, *Howard 10815* (GH), *10818* (GH), *10890* (GH); Large Island, *Howard 10965* (GH); Mayero, *Broadway 5748* (TRIN), *Howard 11038* (GH); Mustique, *Howard 11223* (GH); Petit Martinique, *Howard 10935* (GH); Petit St. Vincent, *Howard 10896* (GH); Tobago Cays, *Howard 11024* (GH); Union, *Howard 10988* (GH). **Grenada:** St. Georges, *Broadway 1760* (B, FM, GH, NY), *1795* (FM, GH, NY), *Howard 10692* (GH); Grand Anse, *Broadway 2503* (FM, MO), *3361* (B, M); Sauteurs, *Howard 10705* (GH). **Trinidad:** Caledonia Island, *Hart 5834* (TRIN). **Tobago:** The Lodge, *Broadway 4019* (B, FM), *Howard 10453* (GH), *10454* (GH), *10458* (GH). **Carrera Island:** *Broadway s.n.* (NY). **Margarita:** *Johnston 274* (GH).

In the original description of *Coccoloba novogranatensis*, Lindau cited a Karsten collection from Sabanilla, Colombia, and a Triana specimen

without specific locality. In the Berlin Herbarium there are two sheets representing this species, but in contrast to his usual practice, Lindau did not indicate by abbreviation, or otherwise, his choice of a type. The Triana specimen is a fragment of a leaf in a packet with a pencil sketch of a fruit on the packet. The Berlin sheet attributed to Karsten consists of two flowering fragments of different ages. It would appear that the Karsten specimen in Berlin could be considered the holotype; however, when botanists from the Field Museum photographed this specimen, temporary annotations were placed on the "Karsten" sheet to indicate that one of the two flowering fragments was a Karsten collection and the other a Triana collection. The labels have since been removed. Thus I have been unable to verify whether this sheet is truly a mixed collection. Both flowering fragments apparently represent the same species, but I am unable to state positively which is the type. It is likely that additional Karsten material from Colombia exists in other herbaria and that a lectotype should be selected at a future date.

I have seen in the herbarium of the Muséum National d'Histoire Naturelle in Paris two full sheets of *Triana 978*, a number cited by Lindau. The collection was made between Anapoima and Apulo, Province of Bogota in Colombia. Each of the two sheets has a branch with young flowers and a second branch in fruiting condition. No fruits remain with the specimens.

I have not seen additional material collected by Karsten. Lindau indicated that his specimens of this species came from Berlin, Leningrad and Vienna. The first two collections are intact and I have seen all the material. The Vienna collection of this genus was destroyed during World War II. While it is possible that Karsten material exists in some other herbarium, it seems practical at this time to designate *Triana 978* as the type collection and one of the two sheets in the Paris herbarium is selected as the lectotype.

In the herbarium material from the Muséum d'Histoire Naturelle in Paris there are three additional sheets to be referred to *Coccoloba novogranatensis*. All were collected by Pleé. Two sheets, one with a printed and one with a script label, were collected at Maracaibo (Venezuela). The third carries a printed label "Martinique." I cannot distinguish the specimens as distinct and different collections and since *C. novogranatensis* has not as yet been collected in Martinique, I suspect that this sheet too should bear a Maracaibo label.

Urban did not indicate a holotype in his publication of *Coccoloba caribaea*, but the specimen *Broadway 1760* in the Berlin Herbarium is indicated as the type in Urban's handwriting. This collection is in flower and is comparable in all characteristics to the fragments on which Lindau based *C. novogranatensis*. There have been no recent collections assigned to *C. novogranatensis*; in fact, the name has been overlooked in recent years. A number of recently described species from Colombia and Peru and from Central America will be assigned in synonymy to *C. novogranatensis* in a later paper.

A large number of *Coccoloba novogranatensis* populations were studied

in the Lesser Antilles and a considerable morphological variation was recognized as being of an ecological nature. The size, color, texture and attitude of the leaves on the shoots seemed to depend upon whether the populations are growing in full sunlight, in shade, in an area subject to salt spray or in moist situations. A similar set of variations has also been recognized in *C. venosa* and collections of these two species from the Lesser Antilles have been confused by various authors. For example, the plants on Mt. Royal in Cannuoan in the Grenadines which John Beard refers to *C. venosa* are more properly referred to this species. *Coccoloba venosa* and *C. novogranatensis* may be readily distinguished by referring to the point of attachment of the petiole to the ocrea.

Coccoloba pubescens L. Syst. ed. 10. 1007. 1759; Hooker, Bot. Mag. *t. 3166.* 1832; Fawcett & Rendle, Jour. Bot. **51**: 123. 1913; Howard, Jour. Arnold Arb. **38**: 227. 1957.

Scortea arbor americana, amplissimis foliis, aversaparte nervis extantibus hirsutie ferruginea refertis; Pluk. Phytographia *t. 222, f. 8.* 1691.

Coccoloba grandifolia Jacq. Enum. 19. 1760.

Coccoloba rubescens L. Sp. Pl. ed. 2. 523. 1762.

Coccolobis pubescens Sandwith, Jour. Bot. **78**: 98. 1940.

Coccolobis antiguensis Sandwith, Jour. Bot. **78**: 98. 1940.

Mature tree to 13 m. tall, d.b.h. 5 cm., much branched above a well-defined trunk; branches terete, swollen at the nodes, the lenticels not conspicuous, tomentose to pilose; ocreae to 1 cm. long, generally completely deciduous, pubescent; leaves of completely mature plants vary considerably in size and shape, the petioles 3–6 mm. long, inserted below the ocreae, densely short-pubescent, the blades broadly orbicular to orbicular-ovate, 4 × 6, 7.5 × 10 cm. long and broad grading into size of leaves of adventitious shoots, rugose or bullate, the apex rounded, the base cordate, the basal lobes rounded and only rarely approximate, sparsely pubescent above to glabrate, densely to sparsely pubescent below or glabrate, the margin undulate, the venation of 5 pairs of primary veins, arcuate to the margin, strongly anastomosing, slightly impressed above, conspicuous and reticulate below; adventitious shoots generally strict and sparsely branched, to 10 m. tall; branches stout, terete, slightly swollen at nodes, strongly grooved or striate; ocreae 2 cm. long, membranaceous and evanescent above, coriaceous and persistent below, the petioles stout 1–2 cm. long, densely tawny pubescent; blades large, generally orbicular except for the terminal leaf, frequently broader than long, 30 × 40, 50 × 80 cm. long and broad, coriaceous, rugose or bullate when mature, thin and plane when young, the apex rounded, the base rounded to cordate, the basal lobes commonly encircling the stem, the terminal leaflet commonly rhombic, longer than broad when mature, densely tomentose, the veins slightly impressed above, all venation conspicuous and reticulate below; midrib and secondary veins persistent pubescent above, the others sparsely pubescent when young, becoming glabrate above, the veins and leaf surface pubes-

cent or becoming glabrate below, the margin irregular, commonly undulate; inflorescence terminal, often stout, the basal ocreae to 7 mm. long, membranaceous, the peduncle to 1.5 cm. long, the rachis minutely and often densely puberulent, 10–18 cm. long on mature shoots, to 45 cm. long on adventitious shoots, the bracts broadly ovate, about 1 mm. long, puberulent, the ocreolae membranaceous spreading, 1 mm. long, minutely puberulent or glabrate; staminate flowers 2–4 at each locus, the pistillate flowers 1–3 at each locus, the pedicels 2–3 mm. long, the hypanthium 0.6–1 mm. long, the perianth lobes broadly orbicular, 1.5 mm. long, 2 mm. wide, puberulent, the fertile stamens 2.5 mm. long, the sterile stamens rudimentary 0.5–1 mm. long, the fertile pistil glabrous or rarely slightly puberulent, on the ovary, the sterile pistils glabrous, rudimentary, 0.5–1.5 mm. long; fruit globose to ovoid, 5–6 mm. long and 4.5 mm. in diameter, the fruiting perianth imbricate at the apex, not coronate, the fruiting hypanthium with conspicuous vascular bundles; achene subglobose, dark brown, shining, slightly triradiate at the apex, the fruiting pedicels puberulent, 3–4 mm. long.

DISTRIBUTION: Dominican Republic, Puerto Rico, Virgin Islands and the Lesser Antilles south to St. Lucia and Barbados.

Barbuda: *Ponthieu s.n.* (FM). **Antigua:** Carrs Gut, *Box 301* (US), *1496* (A, US, ISOTYPES of *C. antiguensis*); Macarthy Hills, *Box 1495* (BM, US); Wallings Area, *J. Beard 283* (A, MO), *Howard 11984* (GH); Blubber Valley, *Howard 11863* (GH), without location, *Wullschlaegel 486* (M). **Montserrat:** Cudjoe Head, *Shafer 457* (FM, NY, US); Harris' Lookout, *Howard 11873* (GH). **Nevis:** Ward's Mountain, *Howard 11933* (GH). **Guadeloupe:** Pigeon, *Duss 3379* (US); Désirade, *Stehlé 195* (GH, NY); Deshaies, *Stehlé 2018* (US); Jarry, *Questel 602* (US); Vieux Fort, *Howard 11847* (GH), *11849* (GH); without location, *Duss 1743* (NY), *2193* (FM, GH, MO, NY). **Dominica:** Calibishie, *W.H. & B.T. Hodge 3142* (GH); Pointe Ronde to Milton Estate, *W.H. & B.T. Hodge 2668* (GH); Pointe Baptiste near Calibishie, *W.H. & B.T. Hodge 3499* (GH). **Martinique:** Presqu'ile de la Caravelle, *Egler 39–252* (NY), *Duss 1743* (NY), *Howard 11728* (GH), *11729* (NY). **St. Lucia:** Between Le Toc and Cul de Sac Bay, *Howard 11371* (GH); Vieux Fort, *Howard 11475* (GH). **Barbados:** Turner's Hall Woods, *Eggers 7158* (A).

The growth forms of *Coccoloba pubescens* have been discussed in earlier papers (Jour. Arnold Arb. 38: 229–231. 1957, 39: 37–39, 44–46. 1958). Immature forms with wand-like branches and very large leaves are the most common habit found in the Lesser Antilles. Beard illustrates such growth forms in his publication "Vegetation of the Windward and Leeward Islands" (Oxford Forestry Memoir 21: *f. 32*. 1949). A few isolated mature plants with the smaller leaf type were seen and collected on St. Lucia (*Howard 11475*), Guadeloupe (*Howard 11849*) and Martinique (*Howard 11729*). The variation in the texture, size and pubescence of the leaves within the populations studied in the field will include that described by Sandwith for his species *C. antiguensis*. I have previously placed that species in the synonymy of *C. pubescens* (Jour. Arnold Arb. 38: 231. 1957).

Coccoloba striata Benth. Hooker Lond. Jour. Bot. 4: 626. 1845.

Coccoloba guianensis Griseb. Fl. Brit. W. I. 163. 1859, not Meisner.
Coccoloba grisebachiana Lindau, Engl. Bot. Jahrb. 13: 195. 1890.
Coccoloba pittieri R. Knuth ex Pittier, Man. Pl. Usuales Venez. 355. 1926.

Tree with scrambling branches; branches hollow, striate, glabrous; ocreae membranaceous above, coriaceous and persistent below, strongly ribbed; petioles attached above the base, strongly grooved above, 1.5–2 cm. long, glabrous; blades ovate to ovate-elliptic, 9 × 5.5 to 14 × 8 cm. long and broad, chartaceous, usually turning dark on drying, the apex shortly and obtusely acuminate, the base rounded to cordate or slightly cordate-auriculate, the midrib and primary veins almost immersed above and only slightly prominent below, the primary nerves 6–8 pairs, arcuate and anastomosing near the margin, the ultimate venation densely reticulate; leaves of scrambling shoots broadly ovate to 23 cm. long and 18 cm. broad, on petioles 3 cm. long; inflorescence to 27 cm. long, the rachis thin and glabrous or slightly puberulent, the flowering nodules widely separated in the pistillate plants and less conspicuously so in the staminate plants, the peduncle about 1 cm. long, the bracts ovate to triangular generally 1 mm. long, the ocreolae flaring, scarcely as long as the bracts, the pedicels equalling the ocreolae in the staminate flower; staminate flowers generally 2–4 per nodule, the hypanthium 0.75 mm. long, the perianth lobes ovate to oblong, 0.5 mm. long, the functional stamens with filaments 1 mm. long; pistillate flowers not seen; fruiting pedicels 2–2.5 mm. long, the ripe achenes red, ovoid, about 9 mm. long and 6 mm. in diameter, the apex acuminate, the lobes inconspicuous, the fruit slightly stalked at the base, obscurely 3-angled.

British Guiana: Without specific location, *Richard Schomburgk 1265* (B). **Trinidad:** Mount Tocuche, *Crueger* (TRIN 776-ISOTYPE of *C. grisebachiana*), *Baker* (TRIN 14804), *Freeman* (TRIN 9045), *Britton, Hazen and Mendelson 1262* (GH, NY). **Venezuela:** Carababo, Guaremales, *Pittier 8880* (A, GH, ISOTYPES of *C. pittieri*); Carruao, *Pittier 11847* (A).

This species is distinctive among the other species of *Coccoloba* reported from Trinidad on the basis of the hollow scrambling branches, the attachment of the petioles above the distinctive base of the ocrea and by the widely separated flowering nodules on the inflorescence rachis of the pistillate plants. The extremely fine reticulate pattern of the ultimate venation of the leaves is also characteristic, although this expression is not always seen in the herbarium collections.

One sheet of *Pittier 8880* in the Gray Herbarium collections cited above probably represents an adventitious shoot. A short piece of the stem 9 cm. long contains one node. The stem is hollow and the ocrea extends 5.5 cm. above the apex of the petiole scar and 1.5 cm. from this point down the stem. The ocrea is coriaceous, appressed and deeply bifid. The leaf on the same herbarium sheet is not attached but is oblong in shape and 40 cm. long and 17 cm. broad. The margin is obviously undulate when fresh. Unless this is a mixed collection, which does not seem likely, the dissim-

ilarity of the leaves of fertile and adventitious shoots is as large in this species as in other species of *Coccoloba*.

The material cited above from Trinidad is all from pistillate plants in fruiting condition or with old inflorescence axes. The types of *Coccoloba striata* and *C. pittieri* are staminate plants. There is no question in my mind that these are all conspecific, although I have not seen this species in the field.

Coccoloba paraensis Meisner, based on Spruce and Martius' material from Para and Amazonas, and *C. glaziovi* Lindau, based on a Glaziou specimen collected from Rio de Janeiro, probably represent the same species and should be assigned to synonymy here. Regrettably, I have insufficient material either to include or exclude these species with certainty at the present time.

Coccoloba swartzii Meisner, DC. Prodr. **14**: 159. 1856; Lindau, Engl. Bot. Jahrb. **13**: 157. 1890; Howard, Jour. Arnold Arb. **30**: 420. 1949, **37**: 317–339. 1956.

Coccoloba swartzii var. (?) *portoricensis* Meisner, DC. Prodr. **14**: 160. 1856.
Coccoloba barbadensis Lindau, Engl. Bot. Jahrb. **13**: 148. 1890; Duss, Ann. Inst. Col. Marseille **3**: 166. 1897, not Jacquin.
Coccoloba diversifolia Lindau, Symb. Antil. **1**: 223. 1899; Griseb. Fl. Brit. W.I. 163. 1859, and most recent authors, not Jacquin.

Trees 8 to 20 m. tall; branches terete, the youngest puberulent, becoming glabrate, the nodes slightly tumid; ocreae 10–12 mm. long, the basal portion 3–5 mm. long, coriaceous, persistent, the upper portion membranaceous and deciduous, puberulent to glabrate; leaves of normal shoots with petioles 10–18 mm. long, puberulent to glabrate, the blades ovate to elliptic, 2.2 × 1.3, 7 × 5, 11 × 9, 15 × 7.5 cm. long and broad, coriaceous, usually turning black on drying, glabrous, having pit-like depressions on the upper surface and small glands on the lower surface, the apex acute, often rounded, the base narrowed, rounded or slightly cordate and usually oblique, the margin entire; midrib and veins inconspicuous or flat above, prominent below, the primary veins 6 or 7 pairs, arcuate, anastomosing, the secondary venation conspicuous, reticulate; leaves of adventitious shoots with petioles 1.5–2.5 cm. long, the blades generally ovate to lanceolate 23 × 8.5, 45 × 18.5, to 70 × 25 cm. long and broad, the apex acute to acuminate, the base rounded; inflorescence terminal 10–15 cm. long, the rachis glabrous or with glandular exudate, rarely papillose; staminate flowers in clusters of 3–5 flowers at each node, tightly surrounded by membranaceous ocreolae which form a truncate cylinder after the flowers have fallen, the pistillate flowers borne singly at each node, the bracts ovate 0.5 mm. long, the ocreolae 1.1.5 mm. long, membranaceous, the pedicels shorter than the ocreolae; hypanthium 0.5 mm. long, the perianth lobes 1–1.5 mm. long, the fertile stamens 1–1.5 mm. long, the sterile stamens rudimentary, 0.5 mm. long; fruit ovoid 8–10 mm. long, 6 mm. diameter, the perianth lobes 1–1.5 mm. long and coronate in fruit; achene dark brown.

DISTRIBUTION: Jamaica, the Bahamas, Dominican Republic, Puerto Rico, St. Croix, St. Jan, Virgin Gorda, St. Thomas, Saba, St. Kitts, Montserrat, Nevis, Antigua, Guadeloupe, Dominica, Martinique, St. Lucia and Barbados.

Antigua: Pearl Hill, *Box 975* (US). **St. Kitts:** Mt. Misery, *R.A. & E.S. Howard 11938* (GH). **Nevis:** *R.A. Howard 11921* (GH). **Montserrat:** Central Hills, *R.A. & E.S. Howard 11868* (GH), *11866* (GH), *11871* (GH), *11872* (GH); Gage's Upper Soufriere, *R.A. & E.S. Howard 11882* (GH); Gardu Gut, *Shafer 323* (F, NY, US), *615* (F, NY, US). **Guadeloupe:** Bois de Gombeyre, *Duss 3251* (F, GH, NY, US); Bouillante to Pointe Noire, *R.A. & E.S. Howard 11843* (GH). **Dominica:** Antilles near Marigot, *R.A. & E.S. Howard 11754* (GH); Salybia, *W.H. Hodge 3404* (GH); South Chiltren Estate, *W.H. & B.T. Hodge 1583* (GH). **Martinique:** Casa Pilote, *Hahn 1187* (F, GH, US), *R.A. & E.S. Howard 11712* (GH); Diamant, *Duss 37, 248* (NY); Mt. Pelee, *Duss s.n.* (NY); Montagnes des Trois Flotz, *Hahn 629* (F, GH); Presqu'ile de la Caravalle, *R.A. & E.S. Howard 11727* (GH), *Egler 39–230* (NY); Trois Islets, *R.A. & E.S. Howard 11731* (GH). **St. Lucia:** Castries-Dennery Road, *R.A. & E.S. Howard 11335* (GH), *11329* (GH), *11355* (GH); Gros Piton, *R.A. & E.S. Howard 11506* (GH); Le Toc to Cul de Sac Bay, *R.A. & E.S. Howard 11377* (GH); Vieux Fort, *R.A. & E.S. Howard 11404* (GH). **Barbados:** Turners Hall Wood, *Eggers 7161* (US).

Coccoloba swartzii forma **pubescens** Howard, Jour. Arnold Arb. 30: 420. 1949.

Similar to the species, but the young shoots, petioles, the lower end of the upper leaf surface, especially the midrib, the ocrea and the inflorescence rachis, at least at the base, puberulent to pilose pubescent.

Antigua: Blubber Valley, *Box 1411* (US-HOLOTYPE), *R.A. & E.S. Howard 11860* (GH), *11985* (GH), *11986* (GH); Carr's Ghaut, *R.A. & E.S. Howard 11994* (GH); Orange Valley, *Box 1184* (GH, US); Pelican Bay area, *R.A. & E.S. Howard 11990* (GH); Sugar Loaf Mt., *Box 1543, 1544* (US), *A.C. Smith 10489* (A). **Barbuda:** Codrington Village, *Fairchild 3830* (A, US); Martello Tower, *J.D. Beard 372* (A, MO); without location, *Box 602* (US). **Guadeloupe:** *De Ponthieu 86* (FM).

Coccoloba uvifera L. Syst. Nat. ed. 10. 1007. 1759.

Polygonum uvifera L. Sp. Pl. 365. 1753.
Guaiabara uvifera House, Amer. Midl. Nat. 8: 64. 1922.

Tree of strand areas, 2–17 m. tall, branches terete, stout, papillose to pilose, the nodes not tumid; ocreae rigid, coriaceous at the base, membranaceous at the apex, 3–8 mm. long, papillose to pilose; leaves of normal shoots with petioles stout, 7–10 mm. long, papillose to pilose, the blades orbicular to reniform, 6 × 8, 11 × 13, 13 × 18 cm. long and broad, thick and fleshy when fresh, coriaceous when dry, glabrous and minutely punctate on both surfaces, the apex rounded truncate or emarginate, the base rounded to broadly cordate one lobe often extending around the petiole; midrib and primary veins prominent on both surfaces, frequently brightly colored when fresh, the primary veins 3–5 pairs, usually straight, bifurcate

and weakly anastomosing near the margin, commonly barbate in the axils of the basal veins, the secondary venation minutely reticulate or obscure; leaves of adventitious shoots usually variable in size and shape, commonly obovate; inflorescence stout, 15–30 cm. long, the rachis puberulent; staminate flowers in clusters of 1–7, the pistillate flowers solitary at each locus, the bracts ovate, 1–1.5 mm. long, 2 mm. broad, puberulent, the ocreolae membranaceous, 1 mm. long, puberulent, the flowering pedicels 1–2 mm. long, the perianth yellow-white or greenish, the hypanthium 2–3 mm. long, the perianth lobes 4 mm. long, 3–4 mm. wide, the fertile stamens to 4 mm. long; fruiting pedicels 3–4 mm. long; fruit obpyriform, 1.2–2 cm. long, 8–10 mm. diameter, narrowed at the base, rounded-truncate at the apex, the perianth lobes appressed against the apex of the achene, the perianth rose-purple when mature, the achene black.

DISTRIBUTION: Throughout tropical America along the coasts.

Antigua: Carr's Ghaut, *R.A. & E.S. Howard 11992* (GH); without location, *Box 1434* (A, US). **St. Barts:** *Euphrasen s.n.* (S), *Forsström s.n.* (S), *Questel* 82 (NY). **Montserrat.** Harris' Lookout, *Howard 11874* (GH). **St. Kitts:** *Britton & Cowell 247* (NY), *Sargent s.n.* (A). **Guadeloupe:** St. Francois, *Howard 11787* (GH); without location *Duss 2183* (US). **Dominica:** Carib Reserve, *W.H. & B.T. Hodge 3316* (GH); Cabrites, *Howard 11750* (GH); Hatton Garden, *W.H. & B.T. Hodge 2957* (GH); Pointe Ronde, *W.H. & B.T. Hodge 2686* (GH); Scot's Head, *W.H. & B.T. Hodge 1605* (GH). **Martinique:** Casa Pilota, *Howard 11720* (GH); Presqu'ile de la Caravalle, *Howard 11726* (GH); Salinas Pie Beach, *Egler 39–19* (NY); without location *Belanger s.n.* (B), *Duss 1742* (US), *Sieber 103* (MO, US). **St. Vincent:** Kingshill, *Howard 11125* (GH). **Grenadines:** Bequia, *Dalton for H.H. Smith B–128* (GH); Mayero, *Howard 11041* (GH), *11042* (GH); Petit St. Vincent, *Howard 10912* (GH); Kick 'em Jenny, *Howard 10782* (GH). **Grenada:** Grande Anse, *Broadway s.n.* (FM, GH), *J.S. Beard 203* (A). **Barbados:** Christ Church, *Dash 129* (FM); St. Philip, *Bovell 129* (US); without location, *Curran.* (FM, MO), *Eggers 7347* (A). **Trinidad:** Galera Point, *Broadway s.n.* (A); Monos Island, *Williams* (TRIN). **Tobago:** Buccoo Bay, *Elmore V–4* (FM); Crown Lands, Palo Saco, *Russell* (TRIN *13071*); Farm Road, *Williams* (TRIN *11143*); Lower Scarborough, *Broadway 3617* (FM, S); Mt. St. Georges, *Howard 10480* (GH); Speyside, *Turley* (TRIN 15244).

Coccoloba venosa L. Syst. Nat. ed. 10, 1007. 1759; Fawcett & Rendle, Jour. Bot. **51**: 123. 1913.

Uvifera arbor americana, fructu aromatico punctatus, Pluk. Alm. 394. *t. 237, fig. 4.* 1696, as to leaf only.
Coccoloba punctata L. Sp. Pl. ed. 2, 523. 1762.
Coccoloba nivea Jacq. Hist. Stirp. Amer. 115, *pl. 78.* 1763; Enum. Pl. 19. 1762.
Coccoloba excoriata Duss, Ann. Inst. Col. Marseille **3**: 168. 1897. not L.
Guaiabara venosa House, Am. Midl. Nat. **8**: 64. 1922 as *Guaibara.*

Trees to 15 m. tall; branches terete, glabrous, the nodes not tumid; ocreae membranaceous, deeply cleft, acuminate on one side, or truncate, to 2 cm. long; glabrous or with flattened glands; leaves of normal shoots with petioles 5–10 mm. long, glabrous, the blades oblong-lanceolate to elliptic, 8 × 4, 10 × 4.5, 16.5 × 6.5, 21 × 9, 27 × 10.5 cm. long and

broad, membranaceous, glabrous except for clusters of hairs in the axils of the veins, sparsely glandular below, the apex short-acuminate, the base narrowed and slightly cordate or cuneate or obtuse; midrib and primary veins slightly prominent on both surfaces, the primary veins 8–13 pairs, straight or arcuate, bifurcate and anastomosing at the margins; leaves of the adventitious shoots about the same size, the internodes much elongate and the ocreae to 4 cm. long; inflorescence terminal or terminal on short lateral branches, the rachis puberulent, angular; staminate flowers in clusters of 2–5, the pistillate flowers solitary, the bracts lanceolate-ovate, to 1.5 mm. long, black, puberulent to pilose or commonly with a fringe of hairs at the apex; ocreolae membranaceous, enlarging with the expanding bud, each flower with an ocreola, to 2 mm. long, the flowering pedicels 1–2 mm. long, glabrous; hypanthium less than 0.5 mm. long, the perianth lobes broadly ovate, 1.5–2 mm. long and broad, slightly unequal, the fertile stamens to 1 mm. long; fruiting pedicels 1.5–2.5 mm. long, the perianth lobes fleshy, white or pink, enclosing the black achene, the hypanthium scarcely evident in the fruit, the fruit 3–4 mm. long and broad, the fruit broadly ovoid.

DISTRIBUTION: Cuba (introduced), Hispaniola, Puerto Rico, Jamaica (?), Virgin Islands, Lesser Antilles and Trinidad.

Antigua: Galley Bay, *Box 1081* (US); Morris, *J.S. Beard 351* (A, MO); Wallings, *Howard 11989* (GH), without location, *Fairchild s.n.* (US). **St. Martin:** *Forsström s.n.* (S), *Boldingh 2993B* (NY). **St. Barts:** *Forsström s.n.* (NY, S), *Le Gallo 2371* (A). **Montserrat:** Harris' Lookout, *Howard 11875* (GH). **Tortola:** *Schafer 1125* (US). **Guadeloupe:** Bouillante to Pointe Noire, *Howard 11842* (A); Gourbeyre, *Duss 3250* (FM, NY, US); Riviere, *Stehlé, Quentin & Bena 5313* (US); Les Saintes, *Questel 1763* (US). **Dominica:** Roseau to Canefield, *Hodge 443* (GH, NY, US). **Martinique:** Carbet, *Duss 1744* (NY); Casa Pilota, *Hahn 967* (G, US), *1182* (S), *Howard 11714* (GH). **St. Lucia:** Soufriere, *Howard 11580* (GH). **Grenadines:** Kick 'em Jenny, *Howard 10792* (GH); Isle of Ronde, *Howard 10713* (GH), *10717* (GH). **Grenada:** *Broadway s.n.* (MO, NY, US). **Barbados:** Dodd's Botanical Station, *Waby 131* (FM); Turners Hall Woods, *Gooding 594* (NY), *Dash 262* (NY). **Trinidad:** Castara, *Sandwith 1831* (NY); Cat's Hill Reserve, *Swabey 12535* (TRIN); Galera Point, *Broadway 2788* (BR, FM, GH, MO, NY, TRIN); Guanapo, *Dannouse s.n.* (TRIN); Quinam Reserve, *Williams 12015* (NY, TRIN); Southwest Reserve, *Marshall 12404* (TRIN), *Swabey 12271* (TRIN); Southern Watershed Reserve, *Russell 12261* (TRIN); Toco, *Freeman & Williams 11768* (NY, TRIN). **Tobago:** Mason Hall, *Broadway 4160* (A, FM, GH, MO, NY, S, TRIN), *Howard 10470* (GH); Point opposite Melville Island, *Freeman & Williams 11422* (TRIN). **Little Tobago:** *Swabey 12959* (TRIN).

THE GENERA OF THE NYMPHAEACEAE AND CERATOPHYLLACEAE IN THE SOUTHEASTERN UNITED STATES

CARROLL E. WOOD, JR.

THE TREATMENTS of the ranalian families Nymphaeaceae and Ceratophyllaceae presented here continue a series of studies toward a biologically oriented generic flora of the southeastern United States made possible by the interest and support of George R. Cooley and a grant from the National Science Foundation. The first paper in this series of generic treatments (The genera of the woody Ranales in the southeastern United States. Jour. Arnold Arb. 39: 296–346. 1958) includes a general explanation of the aims and scheme of this work. As noted there, the area covered in these studies is bounded by and includes North Carolina and Tennessee, Arkansas and Louisiana. The pattern of the descriptions, notes and references is the same as outlined and followed in the introductory paper. It may be called to attention again, however, that the descriptions are based upon the species which occur within this area, items in brackets being supplementary and not applying to our plants. The abbreviations of journals follow those of Schwarten and Rickett (Abbreviations of titles of serials cited by botanists. Bull. Torrey Bot. Club 76: 277–300. 1958). References which have not been checked are marked by an asterisk.

The illustration of *Nelumbo* by Dorothy H. Marsh is from living materials obtained through the enthusiastic assistance of Richard A. Eaton and Kenneth A. Wilson.

NYMPHAEACEAE (WATER-LILY FAMILY)

Aquatic perennial [or annual] rhizomatous herbs, with alternate cordate to peltate floating or emersed leaves with involute vernation, and solitary, axillary, perfect, at least partially cyclic flowers. Plants usually with air-spaces, latex, vascular bundles without cambium or vessels, the leaf-tissues (especially) often with sclereids. Sepals 3–6[–12], green to petaloid, free or slightly united, hypogynous [in ours]. Petals 3-many, showy and colored, to stamen-like, free [in ours], hypogynous, or, with the stamens, inserted on the surface of the ovary, sometimes transitional to stamens. Stamens 3–200, extrorse or introrse; pollen more or less "monocotyledonoid," (monocolpate or derived types) or (in *Nelumbo*) 3-colpate. Gynoecium of [1]2–many carpels, free or united, superior to inferior. Ovules anatropous, many–2–1, pendulous from the top, the walls, or the abaxial suture of the carpels. Fruit a many-seeded berry, a nut, or 1–3 seeded, small and indehiscent. Seeds operculate (except *Nelumbo*), with or without an aril; embryo with thick and fleshy cotyledons, small and

with abundant perisperm and little endosperm or (in *Nelumbo*) large and lacking both. (Including Cabombaceae, Nelumbonaceae.)

A family of eight well-marked genera (five of which occur in our area), of very wide distribution in quiet fresh waters. The genera are linked together by the aquatic rhizomatous habit, the usually long-petioled simple leaves (with a strong tendency towards peltation), the solitary, long-peduncled flowers with at least partially cyclic arrangement of parts, the anatropous, pendulous parietal ovules, the presence of air spaces, the latex-producing habit, and the monocotyledonoid vascular bundles. In respect to other characteristics (e.g., pollen morphology, embryology, operculum and other features of seeds, seedlings, anatomy, floral structure, etc.) the relationships are reticulate. Although a large body of literature exists, many of these latter items have been investigated only partially and it is difficult to draw complete comparisons throughout the family. Various divergences occur between the genera, especially in respect to the structure of flower and fruit, these generally being associated with special mechanisms which function in connection with pollination and with the protection, dispersal, and survival of seeds. The structural features of all these plants need further study and interpretation in connection with their biology.

The treatment of Caspary, who regarded the family as composed of three well-marked subfamilies, is followed here. Some authors, however, split the group into three or even five families (in as many as three orders). These latter treatments seem unjustified, particularly in respect to the Cabomboideae (*Cabomba* and *Brasenia*) and to *Euryale*, *Victoria* and *Barclaya*, all of which clearly seem to be linked to *Nuphar* and *Nymphaea*. *Nelumbo*, the single genus of the Nelumboideae, is perhaps the most divergent member of the family, but even this genus may be regarded merely as being specialized in regard to leaves, dispersal mechanism, embryo and pollen. (See also *Brasenia* and *Nelumbo* below.)

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KEY TO THE GENERA OF NYMPHAEACEAE

A. Carpels united, either along their sides or along the outer margins by adnation to a cup-like "receptacle;" stigmas radiate; ovules numerous in each locule; stamens numerous, introrse; fruit an irregularly dehiscent berry, ripening in the water; leaves with a basal sinus. Subfam. NYMPHAEOIDEAE.

B. Perianth wide-spreading, of 4 sepals and 12–32 showy white, pink, blue or yellow petals; carpels sunken in a cup-shaped fleshy receptacle or hypanthium on the outer surface of which petals and stamens are in-

serted; carpels prolonged upward into slender incurved projections (carpellary styles); seeds arillate. ..... 1. *Nymphaea.*

B. Perianth subglobose, of 6 concave yellow (green- or red-tinged) sepals and numerous scale-like or stamen-like "petals" inserted with the numerous stamens on the receptacle beneath the ovary; carpels completely united, the stigmas radiate and sessile on a disc; seeds not arillate. ..... 2. *Nuphar.*

A. Carpels free (although in *Nelumbo* embedded in the receptacle); ovules solitary or 1–3 in each carpel; stamens hypogynous, few to many (3–36) and extrorse to slightly introrse, or very numerous and extrorse; fruits leathery or hard, indehiscent; leaves (at least the floating or emersed ones) peltate, lacking a basal sinus.

C. Perianth of 6–8 segments, the flowers small; receptacle small, with 4–18 free, superior carpels; fruit small, 1–3 seeded; leaves all floating or submersed; plants more or less coated with mucilage. Subfam. CABOMBOIDEAE.

D. Plants with dissected, opposite submersed leaves and small, peltate floating leaves; perianth petaloid, white or purple; stamens 3–6. ..... 3. *Cabomba.*

D. Plants with only undivided, alternate, peltate floating leaves; sepals persistent, the petals dull purple; stamens 18–36; plants heavily coated with mucilage. ..... 4. *Brasenia.*

C. Perianth of numerous segments, the flowers large and showy; receptacle large, top-shaped, with the many uniovulate carpels sunken separately in cavities in the upper side, only the stigmas protruding; receptacle enlarging greatly in fruit, the carpels maturing into nuts; stamens very numerous, extrorse, hypogynous; all leaves floating or emergent on strong petioles, centrally peltate, large, glaucous; plants lacking mucilage. Subfam. NELUMBONOIDEAE. ..... 5. *Nelumbo.*

Subfam. NYMPHAEOIDEAE Casp.

1. **Nymphaea** L. Sp. Pl. 1: 510. 1753, partim, emend. J. E. Smith in Sibth. & Smith, Fl. Graec. Prodr. 1: 360. 1808–9, nom. cons.

Perennial rhizomatous aquatic herbs with floating ovate to orbicular leaves, cleft at the base, the submerged stipulate petiole inserted at the base of the deep sinus; aerial leaves exceptional; submersed leaves often present, filmy and delicate. Flowers solitary, showy, white (to pink), blue or yellow, borne either at the surface of the water or raised above it. Sepals 4, nearly free, one completely outside the others; petals 12–ca. 32, in whorls of 4, 8, 8 (in subg. BRACHYCERAS), or 4, 8, with the arrangement of petals within these not clear (in subg. NYMPHAEA), in this last the petals often transitional to stamens. Stamens numerous, 50–150, introrse, with or without an appendaged connective. Gynoecium of 7–25 carpels, apocarpous or syncarpous, in a circle abutting and adnate to a central prolongation of the floral axis and sunk in the cup-shaped fleshy receptacle (or hypanthium?), upon the outer surface of which petals and stamens are inserted, and produced above it as "carpellary styles;" upper surfaces of carpels stigmatic to form a broad, concave radiate stigma. Ovules numerous, anatropous, pendulous from the sides of the ovary

locules. Fruit an irregularly dehiscent spongy berry, ripening under water; seeds 1–many per carpel, hard, operculate, embedded in mucilage and each surrounded by a bell-shaped floating aril, embryo small, with 2 equal fleshy hemispherical cotyledons, embedded in a thin layer of endosperm and abundant perisperm. (*Castalia* Salisb., nom, rejic.) TYPE SPECIES: *N. alba* L. (From the Greek and Latin, *Nymphaea*, a water-lily, from *Nympha*, goddess of waters, meadows and forests.) — WATER-LILIES, POND-LILIES, WATER-NYMPHS.

A genus of about 35 species of very wide occurrence (lacking in New Zealand and the Pacific slope of North America) in quiet, fresh (rarely brackish) waters. Represented with us by three species in two of the five subgenera.

Subgenus BRACHYCERAS Casp., characterized by carpels free at the sides, thick, fleshy carpellary styles, and appendaged stamens, and including about 12 species of the tropics and subtropics, occurs in our area as *N. elegans* Hook., a pale-violet-flowered species of southern Florida, the West Indies and Mexico. The sepals and 4 outer petals persist, becoming turgid in fruit.

Subgenus NYMPHAEA (Subg. *Castalia* DC.) characterized by carpels united at the sides, ligulate carpellary styles, obscurely veined sepals, and outer stamens with petaloid filaments, includes about 7 species, all of the northern hemisphere. In our area the subgenus occurs as the yellow-flowered *N. mexicana* Zuccarini (*N. flava* Leitner), $2n = 56$, of Florida, southern Louisiana, Texas, and Mexico, one of the most restricted in range, and the white-flowered *N. odorata* Ait., a quite variable species. This latter occurs both as the typical form and the much larger var. *gigantea* Tricker (*Castalia lekophylla* Small). Some authors also recognize var. *stenopetala* Fern. and var. *minor* Sims. In view of this diversity and the two chromosome levels recorded for this species ($2n = 56$, 84), further critical studies of *N. odorata* are needed. A perhaps parallel case is the complex *N. alba* L., of Europe, in which 84, 105, 112, and 160 chromosomes have been reported.

Flowers of all species are proterogynous. Some are self-fertile, others self-sterile. Our species are all day-flowering; at the latitude of Philadelphia Conard records the flowers of *N. mexicana* as open for each of 2 days from 10–11 A.M. to 3–4 P.M.; those of *N. odorata* open for 3 or 4 days from 6–7 A.M. to 12–1 P.M.; and those of *N. elegans* open from 7–8 A.M. to 12–1 P.M. When receptive, the stigmatic cup is filled with a sweetish, watery liquid. No nectar is secreted (although some species are very fragrant); insects visit the flowers for the abundant pollen.

Numerous hybridizations (particularly within subg. BRACHYCERAS and subg. LOTOS) since about 1850 have produced many showy horticultural plants. Crosses between members of subg. NYMPHAEA have resulted in hardy forms (all sterile) with white, yellow, pink, orange or red flowers. Natural hybrids occur within this subgenus where two or more species grow in the same pond. All attempts to cross species of different subgenera

have failed; within a subgenus interspecific hybrids may be either sterile or fertile. Recorded chromosome numbers range from 28 to 224. The chromosomes of plants used in hybridization work apparently have not been determined. One of the smallest-flowered species (*N. tetragona* Georgi) and one of the largest-flowered (*N. gigantea* Hook.) are both high polyploids ($2n = 120$ and 224, respectively)!

Nymphaea mexicana spreads rapidly by runners and produces on geotropic shoots hibernating bodies or "brood bodies" which consist of a cluster of fleshy roots more or less resembling a "hand" of bananas. Rich in starch, these brood bodies are an important duck food. *Nymphoides aquatica* (Walt.) Kuntze (Gentianaceae) produces similar clusters of fleshy roots at the base of the inflorescence; the two are often confused.

The nomenclatural confusion centering around the application of the name *Nymphaea* to this genus or to that now known as *Nuphar* J. E. Smith has resulted in the conservation of both of these names in the sense in which they are used here.

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2. **Nuphar** J. E. Smith in Sibth. & Smith, Fl. Graec. Prodr. **1**: 361. 1808–1809, nom. cons.

Perennial aquatic herbs with stout, creeping rootstocks, emersed, floating or submersed narrowly lanceolate to orbicular entire leaves with a deep sinus at the base; submersed leaves thin and delicate. Sepals usually 6[5–12], the 3 outer greenish to yellowish, the inner yellow, tinged with red or green. "Petals" numerous, linear to oblong, thick, stamen-like or scale-like, bearing a nectary on the outer surface and inserted with the very numerous introrse stamens on the receptacle under the ovary. Gynoecium of 5–23[–30] carpels, resembling that of *Papaver*, with a stigmatic disc, each carpel with a stigmatic ray; ovary multilocular, with numerous ovules on the inner walls. Fruit an ovoid to columnar berry, dehiscing irregularly by the swelling of a gelatinous covering of the seeds; seeds usually ovoid, yellow to brown, opening by a small operculum, lacking an aril. Embryo with 2 fleshy cotyledons. Pollen monocolpate, oblate-sphaeroidal, spiny. $2n = 34$. (*Nymphaea* L. partim, emend. Salisb. and *Nymphozanthus* L. C. Rich., nom. rejic.) TYPE SPECIES: *N. luteum* (L.) Sibth. & Smith. (The name from Greek *nouphar*, the flowers of a medicinal plant mentioned by Dioscorides, perhaps *N. luteum*.) — SPATTERDOCK, COW-LILY, YELLOW POND-LILY.

Perhaps 19 species in North America, two in Europe and several poorly known in eastern Asia; probably about 14 in our area, but some of these not well understood. The group is taxonomically difficult, especially from herbarium materials, in which the features of the plants are not well re-

tained. Ecological and ontogenetic variations add to the difficulty. Entire populations need study; specimens should be preserved in liquid and carefully pressed flowers and adequate notes made in the field. Taxonomic characters used in the group include habit; shape and pubescence of leaf-blades; cross-sectional shape of petioles; presence or absence of submersed leaves and their shape; number of sepals and color, shape and size of "petals;" shape of pistil; lobing, rays and color of stigmatic disc; shape and coloration of fruit; and color, size and indument of seeds. Special efforts should be made to press open flowers carefully and to record variation in numbers of stigmatic rays; at least some discs should be pressed separately and longitudinal sections of pistils and fruits are valuable.

All of the chromosome counts made thus far indicate a genus with a uniform chromosome number of $2n = 34$. Largely sterile hybrids are known between the European *N. pumilum* and *N. luteum*, between *N. advena* and *N. sagittifolium*, and between *N. variegatum* and *N. microphyllum* (of the northern U. S. and Canada). (This last also exists in a fertile form, *N.* × *rubrodiscum* Morong.) Where *N. advena* and *N. variegatum* overlap in range (e.g., southern Michigan) intermediate plants are known, but these have not been studied in detail. The existence of hybrids of this kind has led to the treatment of the European and American representatives of the genus as a single variable species with 9 subspecies. Most entities appear to be definite units which maintain themselves both ecologically and geographically, however.

The flowers are proterogynous and are visited by pollen-collecting insects (sweat bees, flies and beetles) which work over the introrse anthers exposed by the recurving of the filaments as anthesis proceeds. The fruit ripens generally below the surface of the water, splitting irregularly, the carpels tending to separate and float as decay of the berry occurs.

As in *Nymphaea*, long known for the occurrence of sclereids in blades and petioles, bizarre stellate sclereids occur at the intersections of vertical diaphragms in the petioles. Both genera have been the subject of numerous anatomical and physiological investigations, a great many of which have dealt with the European *Nuphar luteum* and *Nymphaea alba*.

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Subfam. CABOMBOIDEAE Casp.

3. **Cabomba** Aubl. Hist. Pl. Guiane Franç. **1**: 321. *t. 124*. 1775.

Strictly aquatic herbs with opposite submersed leaves and sometimes a few alternate floating leaves. Roots adventitious from the nodes. Sub-

mersed leaves petiolate, the blade divided into 5–7 parts at the summit of the petiole, each part divided dichotomously and trichotomously several times into many long, narrow segments. Floating leaves (when present) peltate, small, narrow and tapered to both ends, or narrow and forked [or resembling miniature leaves of *Brasenia*]. Flowers borne singly on long axillary peduncles, the perianth white or purple [or yellow], sepals 3 and petals 3, slightly united near the base. Petals clawed, the blade often auriculate. Stamens 3–6, extrorse, the pollen 1-sulcate. Carpels [1]2–4, free, elongate, with small terminal stigmas; ovules usually 3, one on the adaxial, one on the abaxial suture and one on the wall near either. Fruit indehiscent; seeds 3, pendulous, operculate, covered with elongated processes; embryo as in *Nymphaea*, small. TYPE SPECIES: *C. aquatica* Aubl. (The name presumably a barbaric one.) — FANWORT, WATERSHIELD.

Seven species of warm and temperate regions of the New World. Two species, *C. caroliniana* Gray ($2n = 24$) and *C. pulcherrima* (Harper) Fassett, in our area. *Cabomba caroliniana*, with yellow-based white petals rounded at the summit, ranges from south-central Texas to southern Florida, northward to Kentucky, southern Michigan and along the Atlantic coast to New York, Connecticut, and southeastern Massachusetts. Often used as an aquarium plant, this species appears to be adventive north of Virginia. *Cabomba pulcherrima*, with purple, emarginate perianth segments, occurs at low altitudes from southwestern South Carolina to southwestern Georgia and adjacent Florida. The terminal divisions of the leaves of both species have spathulate tips.

As an aquarium plant *Cabomba* is most likely to be confused with *Limnophila* (*Ambulia*) *heterophylla* Benth. (Scrophulariaceae), which has sessile ternate leaves with the segments pinnately divided.

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4. **Brasenia** Schreb. Gen. Pl. ed. 8. 1: 372. 1789.

Aquatic herbs with floating, alternate, long-petioled, elliptic, centrally peltate leaves and small, solitary, axillary dull-purplish flowers. Rhizome small, bearing leaves and axillary runners which creep on the surface of mud, root at the nodes, and produce leafy branches and other runners.

Submersed leaves present, at least in seedlings. Submersed parts of plant heavily covered with a mucilaginous jelly. Sepals 3–4, colored within, persistent. Petals 3–4, linear, sessile. Stamens 18–36, the filaments filiform, and anthers slightly introrse; pollen 1-sulcate. Carpels 4–18, free, oblong-ovate, the ovules 2 in each, anatropous, pendulous from the abaxial suture. Fruit clavate, indehiscent, with 1 or 2 small, dull, grayish white, operculate seeds. TYPE SPECIES: *B. Schreberi* Gmel. (Origin of name not explained by Schreber.) — WATER-SHIELD, WATER-TARGET, PURPLE BONNET, PURPLE WEN-DOCK.

A single species widely but sporadically distributed in ponds and slow streams in the West Indies, Mexico and Central America, Florida to Texas, north to Prince Edward Island, southern Quebec, southern Ontario, and Minnesota; also Idaho, California to British Columbia and Alaska; eastern Asia, Australia and Africa.

This curious plant with centrally peltate leaves is clearly linked to *Cabomba* through leaves, floral structures, and pollen morphology. Both plants are sometimes treated as a separate family, the Cabombaceae. Seeds, seedling ontogeny, pollen morphology and embryology, as well as structural features, do not bear out such a segregation, however. It may be noted that in *Brasenia* the mode of seed germination and the early seedling stages are essentially the same as in *Nymphaea* and *Nuphar*. The first leaf is awl-like, the second narrowly oblong with the petiole at the margin at the lower end. Subsequent leaves are eccentrically peltate, then centrally peltate, a total of 6–9 submersed leaves being produced before the first characteristic floating leaves.

The submersed parts of the plant are notable for the extremely heavy covering of mucilaginous jelly, the secretion of numerous ephemeral glandular hairs (found also, but to a lesser degree, in the other genera, with the exception of *Nelumbo*). Specimens should be prepared with waxed paper, for the leaves become quite brittle in drying and adhere firmly to newsprint.

Dianthesis has been reported in *Brasenia* in Japan by Tokura (cf. H. L. Mason, Fl. Marshes Calif. 491. 1957). The proterogynous flowers are raised above the water and are open for the first time from about 6 to 9 A.M., are then drawn into the water to reappear the following morning when the pollen is shed, and finally are withdrawn again. (Cf. dianthesis in *Persea* [Lauraceae]).

In the southern part of our range the plant is evergreen, but at least in the northern United States it produces in autumn winter buds which absciss from the parent plant and overwinter at the bottom of the pond. These reddish, translucent bodies consist of the thickened stem-tip with dwarf leaves with thickened petioles and the characteristic gelatinous covering. Dispersal is effected not only by the winter buds but by the fruiting peduncles which become detached and float.

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Subfam. NELUMBONOIDEAE Casp.

5. **Nelumbo** Adans. Fam. Pl. **2**: 76. 1763.

Aquatic herbs with fibrous roots borne at the nodes of slender horizontal vegetative rhizomes and thickened storage rhizomes, and with large, dimorphic (floating and emersed) peltate leaves and large yellow or pink flowers borne on stout peduncles well above water. Perianth of ca. 14–26 petaloid tepals, the outer 2–5 persistent (and thus calyx-like), the inner caducous in 2–4 days. Stamens ca. 200, with a conspicuous fleshy terminal appendage, extrorse, spirally inserted; pollen tricolpate. Carpels usually 12–28 (9–39), borne singly in cavities in the pithy obconical receptacle, basally attached, flask-shaped, the ovary oblong-cylindric, completely immersed, the style short, neck-like, the stigma circular, centrally depressed; ovule solitary in each carpel, anatropous, pendulous from the top of the locule. Carpels becoming in fruit acorn-like very hard-walled nuts in the greatly enlarged receptacle. Embryo with only a rudimentary primary root, filling the fruit with two large fleshy cotyledons which inclose in a delicate stipule-like sheath a green plumule with two peltate involutely folded leaves and two rudimentary leaves. Seedling floating upon germination; all roots adventitious. $2n = 16$. (*Nelumbium* Juss.) Type species: *N. nucifera Gaertn.* (Name derived from the Ceylonese name for *N. nucifera*.) — Yellow lotus, Yellow nelumbo, Great yellow lily, Pond-nuts, Water-nut, Water-chinquapin, Wonkapin, Yonkapin, Yockernut, Duck acorns, Rattle-box, Alligator buttons.

Two species, *N. lutea* (Willd.) Pers. (West Indies, Central America, Florida to Texas, and locally northward to southern New England, New York, southern Ontario, Minnesota and Iowa) and *N. nucifera* Gaertn. (China to Australia, India and Persia and introduced and established

locally through cultivation in the United States). The former species has sulfur-yellow to white flowers and nearly spherical fruits, the latter pink to white flowers and somewhat larger ellipsoidal fruits.

Nelumbo lutea is one of our showiest and most interesting native plants. The greatly enlarged top-shaped receptacle with numerous separate carpels is a unique dispersal mechanism. The petals fall after 2–4 days leaving the

FIG. 1. **Nelumbo.** a–p, *N. lutea*: a, habit, × 1/20; b, flower-bud, × ¼; c, flower with petals removed, sepals persistent, × ½; d, stamens — note extrorse dehiscence, appendages, × 1; e, receptacle at anthesis, the stigmas of carpels protruding, × ½; f, receptacle and carpels, vertical section, × ½; g, carpel at anthesis, × 2; h, carpel, vertical section, with pendulous anatropous ovule, × 2; i, receptacle with nearly mature green fruit, vertical section, × ¼; j, dry receptacle with mature fruit, × ¼; k, green fruit at maximum size, × 1; l, mature fruit, the ovary wall sclerified, × 1; m, embryo from mature but green fruit, one cotyledon removed — note absence of hypocotyl and radicle, × 2; n, seedling with two leaves — note eccentric peltation, involute vernation, adventitious roots, × ½; o, seedling with four leaves (only bases of petioles numbered in sequence shown), the fruit coat removed — note distribution of roots, beginning of rhizome, × ½; p, tuber (a single swollen internode) with terminal bud and leaf-bud to right, × ¼; f, i, semi-diagrammatic.

outermost 4–5 tepals which persist into fruit. Within a few days the peduncle bends just below the receptacle, tilting it first to about 45 degrees and later to an almost horizontal position. As the fruits near maturity the receptacle is returned to an upright position, but later is bent downward through 180 degrees. The dry receptacle breaks off, falls into the water and floats with the cavities downward. The individual fruits shrink greatly (½–⅔ their volume) in ripening and the ovary wall becomes very hard and impermeable. Germination of fully ripened fruit may thus be greatly delayed. (*Nelumbo* seeds are the longest lived of any known; roughly 1000-year-old seeds of *N. nucifera* from peat beds in the Pulantien basin of southern Manchuria have germinated consistently.) The fruits strongly resemble those of the chinquapin, *Castanea pumila*, in appearance and the very edible cotyledons (the green plumule is bitter) taste much like those of the same plant.

The plant grows best in organic soil in water up to 6(8) feet deep and spreads as much as 50 feet radially each year by slender runners with internodes up to 5 feet long, the longest of any plant in our flora. It may thus under favorable conditions cover acres crowding out other aquatic vegetation and becoming a pest. The roots are entirely adventitious in 6 groups at the nodes, where lateral branching also occurs. In autumn one or two nodes at the growing tip develop into enlarged banana-like tubers 8–28 cm. long, the overwintering structures from which growth proceeds the following spring. The tubers of both species are highly edible: *N. lutea* was planted by the American Indians for both seeds and tubers and *N. nucifera* is widely cultivated in Asia for the same items.

Although a unique plant, *Nelumbo* appears to be related to the other Nymphaeaceae, differing from them primarily in the seed-dispersal mechanism, the more fully developed embryo (an enlarged and somewhat more specialized version of that of *Nymphaea* and *Nuphar*), the elimination of all submersed leaves, the more completely peltate leaves, and the tricolpate pollen. It is notable that in the leaves there are usually about 25 main veins, all but one of which branch dichotomously, this last being simple. Seedling leaves are apiculate at the end of the simple vein and are eccentrically peltate in the opposite direction, indications of the derived and specialized nature of the centrally peltate leaves which have proceeded to an evolutionary level beyond *Brasenia* (q.v.). Leaf vernation is involute as in the other genera. *Nelumbo* is placed by some in a separate family (Nelumbonaceae Dumort., 1829; Nelumbiaceae Lindl., 1836), or even in a separate order, but it seems better for the present to retain the genus in the Nymphaeaceae in the status accorded it by Caspary.

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CERATOPHYLLACEAE (HORNWORT FAMILY)

The family includes only a single small genus, *Ceratophyllum* L., of nearly cosmopolitan distribution, the plants growing entirely submerged in quiet, fresh waters. The group is easily recognized by the rather brittle and rough, whorled, dichotomously dissected leaves, the minute imperfect flowers, each solitary in the axil of one leaf of a whorl, the equally solitary branching, and the complete lack of roots.

Ceratophyllum was first placed near the Nymphaeaceae in 1837 by Asa Gray, largely on the basis of comparisons drawn with *Nelumbo* [itself highly specialized but mostly along other lines], the chief points being the simple, one-seeded ovaries, the pendulous orthotropous, exalbuminous seeds, the large and fleshy cotyledons, and the unusually developed plumule. Unfortunately, the most strongly emphasized evidence, the ovule, is not orthotropous in *Nelumbo*, *Brasenia* and *Cabomba*, but anatropous. However, Strasburger and others have maintained the same position for the Ceratophyllaceae, citing the convex receptacle, the numerous extrorse stamens, the superior ovary with the single pendulous parietal ovule, and the details of embryogeny (which seem to agree well with Nymphaeaceae). It may be noted that the stamens of *Ceratophyllum* seem to be spirally (not cyclicly) arranged, that the orthotropous ovule has but a single integument (instead of the two usual in Ranales) and that the pollen has lost all features which might be used as an indication of the relationships of the genus

1. **Ceratophyllum L.** Sp. Pl. **2**: 922. 1753; Gen. Pl. ed. 5. 428. 1754.

Aquatic herbs with whorled dissected leaves; monoecious, with minute, sessile, axillary flowers lacking a perianth but with an 8–12-cleft involucre

in place of a calyx. Plants entirely submerged, branching, a single branch produced at a node. Roots lacking (even in the embryo) but leafy branches sometimes modified as "rhizoids." Leaves 6–10 at a node, rather rigid, 1–4-dichotomously dissected, with two rows of minute teeth along the upper side of the ultimate segments, tipped by two bristles, usually with a purplish hair of tannin-filled cells between. Flowers usually solitary in the axil of one leaf of a whorl. Staminate flowers with an involucre of 8–12 segments, slightly united at the base, each tipped with a purplish hair, with a convex receptacle and 10–20 extrorse, 4-locular stamens with large, sessile, often 2-cuspidate anthers; pollen large, nearly smooth, thin-walled, acolpate. Pistillate flower of a solitary pistil with involucre, the style filiform, oblique, the stigma a lateral pocket, the ovary ovate, 1-locular, with a single orthotropous 1-integumented suspended ovule; embryo sac development normal (Polygonum type). Fruit an achene tipped by the indurated persistent style [or its base] and often with additional basal or marginal spines. Seeds filling the fruit, nucellar tissue forming the only seed coat, with a large embryo with 2 ovate cotyledons, a well-developed plumule of several nodes with simple or forked leaves, and lacking a hypocotyl and radicle; endosperm scant or lacking. TYPE SPECIES: *C. demersum* L. (The name from Greek, *keras*, a horn, and *phyllon*, leaf, in reference to the stiff, divided leaves.) — HORNWORT, COONTAIL.

Six or more species, three of which occur in our area: *C. demersum* L., of very wide distribution, from Canada to Argentina and also in Europe, Asia, Africa, and perhaps Australia; *C. echinatum* Gray, distributed from Quebec to Michigan and south to Florida and eastern Mexico; and *C. floridanum* Fassett, known only from the Florida Keys.

The genus is almost completely adapted to an aquatic life. The plants lack cuticle, stomata and roots (even in the embryo, the anchoring function being taken over by leafy branches which grow into the mud); both xylem and phloem are reduced, mechanical cells are lacking, and about a third of the plant is occupied by air spaces. The greatly reduced flowers are borne abundantly and pollination is entirely subaquatic. Fruits develop only if water temperatures are maintained above 80°F (cf. Guppy), a phenomenon which may account for the scarcity of fruiting collections in herbaria. The plants may vegetate indefinitely, however, even under ice in winter; vegetative reproduction occurs by fragmentation.

Species of *Ceratophyllum* are highly variable and are difficult taxonomically. The principal taxonomic characters used are those of fruits and leaves, the fruits being unarmed, or with either long or short spines at the base and the apex or along the margin, the leaves varying in the amount of forking, width of segments, degree of tapering at base, coarseness and distribution of the teeth. The female flowers are so reduced as to be useless in classification, but stamens need further examination, particularly in connection with their terminal cusps and hairs. Chromosome numbers reported from European plants include 24 in *C. demersum* and 40 and 72 in *C. submersum* L. These, combined with the wide range of morphological

characteristics, suggest that much more needs to be done toward an understanding of the biosystematics of the genus.

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